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JOURNAL OF ANATOMY

CAMBRIDGE UNIVERSITY PRESS

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LONDON: FETTER LANE, E.C. 4



H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1

WHELDON & WESLEY, LTD., 2, 3 AND 4, ARTHUR ST., NEW OXFORD ST., LONDON, W.C. 2

CHICAGO: THE UNIVERSITY OF CHICAGO PRESS

(Agents for the United States and Canada)

BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.

TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

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# JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF  
ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY  
OF GREAT BRITAIN AND IRELAND BY

PROFESSOR EDWARD FAWCETT

UNIVERSITY OF BRISTOL

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ROYAL COLLEGE OF SURGEONS

LINCOLN'S-INN-FIELDS, LONDON, W.C. 2

VOLUME LVII

OCTOBER 1922—JULY 1923

CAMBRIDGE

AT THE UNIVERSITY PRESS

1923

200385-  
5/2/26



Q17  
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J6  
v.57-58



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# JOURNAL OF ANATOMY

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## THE ACTION OF REPEATED DOSES OF X-RAYS UPON THE DEVELOPING CHICK EMBRYO<sup>1</sup>

BY HECTOR A. COLWELL, M.B., D.P.H.,  
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### INTRODUCTION

It was not until nearly ten years after the first demonstration of the X-rays in 1895 that work dealing with their action upon developing forms was published. The earliest experiments were those of Perthes upon the ova of *Ascaris megalocephala*, which appeared in 1904; broadly stated, he found that exposure to the rays resulted in delayed development and the production of abnormal forms.

Bordier in 1905 exposed young larvae of the common silkworm and found inhibitory effects upon subsequent development, as did also Hasebroeck, while experimenting upon young forms of other species of Lepidoptera. Hastings, Beckton and Wedd, in a series of observations carried out upon silkworms from 1909 to 1911, which extended over three cycles of their life history, observed generally an inhibitory effect of the rays upon development.

In 1904 Gilman and Baetjer observed temporary stimulation in the development of the eggs of *Amblystoma* as a sequel to irradiation, but in spite of this the resulting forms were abnormal.

Bardeen in 1907–1911 published an extended series of observations upon the action of the X-rays upon amphibian ova, paying particular attention to the susceptibility of the embryos at different stages of development. For this purpose amphibian ova—toad and frog—offer many advantages, since artificial fertilisation of ova removed from the female animal can be readily effected by the addition of an emulsion of the carefully “teased” testis. Bardeen’s experiments comprised irradiation of unfertilised ova, of spermatozoa, and of fertilised ova at different stages of development. He found that spermatozoa, unimpregnated ripe ova and recently fertilised ova were highly susceptible to the rays, that their susceptibility decreases in the second hour after fertilisation, rapidly increases to a maximum in the earlier cleavage stages, and greatly decreases during the stage of gastrulation. Bardeen’s results are given with remarkable fullness and detail and to be fully appreciated the original memoirs must be consulted.

<sup>1</sup> The expenses of this research were partly defrayed by a grant from the Medical Research Council.



Passing now to the consideration of chick-embryos, the first experiments upon the effects of exposure to the X-rays were those of Gilman and Baetjer in 1904. Here the observers recorded an initial acceleration of development, followed by retardation and the production of abnormal forms. Bordier and Galimard in 1905 obtained inhibition of development as a result of exposure, as also did Gaskell in 1911.

In the case of developing mammals, the results of exposure to the X-rays were in all cases found to be deleterious, whether the exposure took place before birth (by exposure of pregnant females) or whether newly born animals were irradiated. The details of experiments of this nature are given, and the results summarised, in a paper by Walter which appeared in 1912.

Before entering upon the details of our present lines of experiment, it may not be out of place to offer a few remarks upon the nature of the X-rays, and their relations to other forms of radiation.

### THE X-RAYS.

Recent investigations have shown that the X-rays consist of electromagnetic waves similar in character to rays of light and ultra-violet rays. From these they differ in having much shorter wave lengths. We are now acquainted with a complete series of undulations, comprising among others the Hertzian waves used in wireless telegraphy, the rays which produce heat, the visible rays, the ultra-violet rays, the X-rays and the gamma rays of radium. From the analogy of such a series of undulations to the visible spectrum, its representation is often referred to as the spectrum of electromagnetic waves, although only a part—and that a very small part—is capable of affecting the retina so as to produce the sensation of light. The unit of measurement commonly used by physicists for describing wave lengths of these undulations is known as the Ångström unit (Å.U.) and measures one ten thousand millionth part of a metre, and is also often referred to for the sake of brevity as a “tenth metre.” This unit is also expressed as  $10^{-10}$  metre or  $10^{-8}$  centimetre.

Now the visible spectrum from deep red to extreme violet, comprises rays which lie between the limits 7200 and 4000 Å.U.; it will be seen that the wave length of the shortest member of the series is about one-half of that of the longest. Such a series of waves are spoken of as forming an “octave” of the spectrum, and thus the visible rays comprise almost one octave of the spectrum of electromagnetic waves. The next group of radiations beyond the visible spectrum consist of undulations of gradually decreasing wave lengths from the ultra-violet rays; these extend over several octaves. Following them is a region which, thanks to the researches of J. J. Thomson, Millikan, Richardson and others has recently been charted. If we reckon rays of the visible spectrum as constituting the first octave now under consideration, well-defined X-rays make their appearance in the tenth octave. X-rays of longer wave lengths than this have been detected in the intervening octaves but, owing to the fact that they are very easily absorbed by matter, the study of their



properties has been rendered extremely difficult. The X-rays which are in common use start about the fourteenth octave, they extend over about three octaves and overlapping them and eventually extending beyond them are gamma rays of radium. The wave length of the most penetrating X-ray yet produced is about  $0.06 \times 10^{-8}$  cm., while the most penetrating gamma ray has a wave length about  $0.01 \times 10^{-8}$  cm.

Thus the X-rays increase in penetrating power as their wave lengths diminish; the "softer" rays, or rays of greater-wave-length will be stopped by, e.g., sheets of metal which allow rays of shorter wave length, or "harder" rays to pass through. Not only is the thickness of the metal screen a factor in stopping the passage of the radiations, but the material of which it consists. Metals of high atomic weight have normally greater stopping powers than metals of low atomic weight.

Now the beam of X-rays from an X-ray tube is never homogeneous, the rays emitted consist of a mixture of radiations of different wave lengths, some "harder" and some "softer." By using a series of metal screens of varying thickness we can gradually cut out the rays of greater wave length while those of shorter wave length are allowed to pass.

This property of metallic screens is made use of in the therapeutic application of the rays and screens of aluminium varying from half a millimetre up to six or eight millimetres or more are interposed between the X-ray tube and the object irradiated according to the requirements of the particular case.

If now we imagine the tube to be running at a fairly constant intensity so that the total out-put of X-rays for a given time is a more or less fixed quantity, the interposition of the screens of gradually increasing thickness will diminish the total amount of rays received by the object irradiated. Thus an object exposed to the rays for two minutes without any screen will receive more total rays, than if a screen be interposed. We are therefore faced with the problem of how to obtain approximately equal doses of radiation when the softer X-rays are cut out by the screen.

In ordinary X-ray therapy the unit of radiation used is very commonly what is known as the Sabouraud-noire pastille dose. It is open to a good many objections but its simplicity of application has secured its extensive use while it is moreover based upon practical therapeutic experience. In brief it consists in the observation of the colour changes produced in a paper disc impregnated with barium platinoeyanide as the result of exposure to X-rays. These discs or "pastilles" (which are also sensitive to light, heat and other physical agencies, so that they have to be kept under fairly stringent conditions) are normally of a pale apple green colour. With exposure to X-rays this tint gradually changes to a yellowish-brown according to the amount of irradiation. The unit known as a "pastille dose" (1 P.D.) was originally determined experimentally by Sabouraud who compared the intensity of irradiation necessary to produce a definite erythema of the skin with the colour changes produced in one of these "pastilles" or discs. A dose of X-rays which just

produced cutaneous erythema was found to produce a reasonably constant tint in the barium platinoeyanide disc and this amount of irradiation forms the unit of pastille dose (P.D.).

Now if screens are interposed between the X-ray tube and the object irradiated, and the disc is placed on the side of the screen remote from the tube, it will, within certain limits, be affected by the total rays passing irrespective of their hardness and its colour changes will depend solely upon the rays which have filtered through the screen. Obviously with increasing thickness of the screens, greater duration of exposure will be necessary to produce the standard change in the pastille.

The colour changes produced by the rays in the platinoeyanide disc are estimated by comparing the tints produced with a series of pieces of standard coloured glass in a simple tintometer, whereby such subdivisions of the pastille dose as four-fifths ( $\frac{4}{5}$  P.D.), half ( $\frac{1}{2}$  P.D.) or a quarter of a pastille dose ( $\frac{1}{4}$  P.D.) can be judged.

#### THE PRESENT EXPERIMENTS

The object in our present series of experiments was to ascertain the action of rays of different degrees of "hardness" upon developing tissues. The chick embryo was selected as the subject of experiment and a series of 36 fertilised eggs were subjected daily to irradiation for a period of 8 days. These were divided into four series which received one pastille dose (1 P.D.), four-fifths ( $\frac{4}{5}$  P.D.), one half ( $\frac{1}{2}$  P.D.) and one quarter of a pastille dose ( $\frac{1}{4}$  P.D.) respectively daily. The same series of screens were used in all the experiments; they were aluminium screens of one half millimetre, one millimetre, and two millimetres, in thickness. This is epitomised in the following table.

Thickness of aluminium screen	$\frac{1}{2}$ mm.	1 mm.	2 mm.
Series 1. 1 P.D.	3 eggs	3 eggs	3 eggs
Series 2. $\frac{4}{5}$ P.D.	3 "	3 "	3 "
Series 3. $\frac{1}{2}$ P.D.	3 "	3 "	3 "
Series 4. $\frac{1}{4}$ P.D.	3 "	3 "	3 "

All irradiated daily for 8 days

The apparatus used was one of the ordinary coils used in the therapeutic X-ray department of King's College Hospital, working with a spark-gap of 6 inches. The current through the primary coil was about 4 amperes at 100 volts, while the current through the secondary was 2 milliamperes. A Coolidge tube was used and the anticathode was 4 inches from the pastille which was, of course, placed on the side of the screen away from the tube. The eggs were covered with a layer of cotton wool and placed in a cardboard box for irradiation.

The first irradiation was given before the eggs were placed in the 37° C. incubator; immediately it was completed they were incubated and only removed for the short time needful for their daily exposure for 8 days. The weather was warm at the time and the eggs were kept covered with cotton

wool during their transit to and from the incubator as well as during incubation and irradiation. They were turned over daily.

On the eighth day the eggs were opened and the embryos carefully transferred to Muller's fluid to which 5 per cent. glacial acetic acid had been added. This fluid was changed daily for one week when the embryos were passed through ascending strengths of alcohol, then through xylol and embedded in the usual way. Serial sections were then cut of each embryo.

*Series 1. 1 P.D. daily for 8 days.*

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(a) $\frac{1}{2}$ mm. filter	(b) 1 mm. filter	(c) 2 mm. filter
(1) Undeveloped	(1) Undeveloped	(1) Undeveloped
(2) Undeveloped	(2) Undeveloped	(2) Undeveloped
(3) Dead and measured 4 mm.	(3) Dead and measured 4 mm.	(3) Dead and measured 4 mm.

*Series 1 (a).* Daily dose, 1 P.D. through  $\frac{1}{2}$  mm. aluminium filter for 8 days.

The only specimen which showed any signs of development was dead, its greatest length was 4 mm. There is marked maceration of the tissues; this no doubt is due to decomposition changes after death. The epithelium is shed both from the surface ectoderm and from the alimentary and respiratory tracts. The central nervous system is completely disintegrated. In the cardio-vascular system the blood shows as a fibrinous clot in which no blood corpuscles can be distinguished. The endothelial lining of the vessels is separated from the muscular wall, but appears as a continuous membrane.

*Series 1 (b).* Daily dose, 1 P.D. through 1 mm. aluminium filter for 8 days. The findings were identical with those obtained in Series 1 (a).

*Series 1 (c).* Daily dose, 1 P.D. through 2 mm. aluminium filter for 8 days.

Here again only one specimen shows any signs of development and its greatest length measures 4 mm. The surface epithelium and that of the alimentary and respiratory tracts is again observed to be shed and disintegrated, doubtless due to post-mortem changes. As regards the central nervous system the walls of the cerebral vesicles are seen to be markedly folded and the tissues macerated. This is probably due to post-mortem changes. The mesenchyme is denser and the tissues less broken up than in the former specimens.

In the genito-urinary tracts signs of development had proceeded further than Series (a) and (b), and tubules and glomeruli can be recognised in the mesonephros. As regards the cardio-vascular system, red blood corpuscles are recognisable in places and the heart is developed but its walls disintegrated.

*Series 2.  $\frac{4}{5}$  P.D. daily for 8 days.*

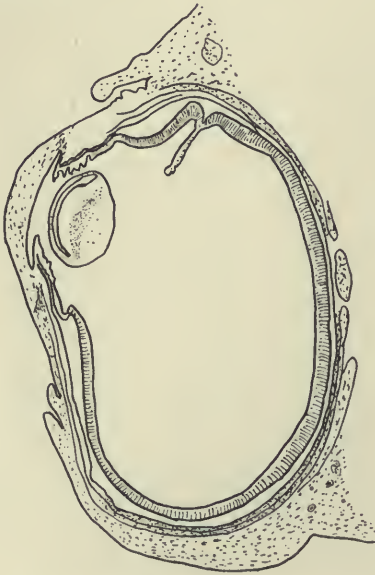
(Average greatest length of normal 8 day chick embryo = 22 mm.)

(a) $\frac{1}{2}$ mm. filter	(b) 1 mm. filter	(c) 2 mm. filter
(1) Undeveloped	(1) Undeveloped	(1) Undeveloped
(2) Trace of embryo apparently of 48 hours development	(2) Dead and measured 10 mm.	(2) Dead and measured 4 mm.
(3) Living and measured 8 mm.	(3) Living and measured 10 mm.	(3) Living and measured 12 mm.

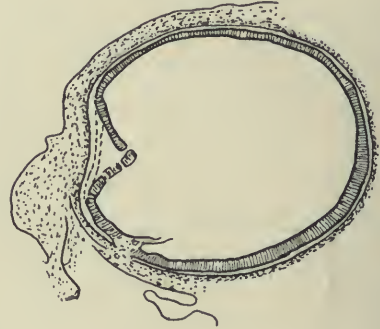


*Series 2 (a).* Daily dose  $\frac{4}{5}$  P.D. through  $\frac{1}{2}$  mm. aluminium filter for 8 days.

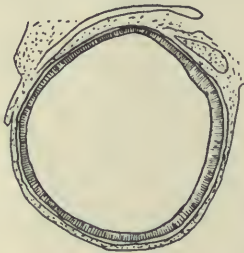
Of the three eggs examined one was undeveloped, one showed a trace of an embryo apparently of 48 hours' development while the third was alive and measured 8 mm. in its greatest length; this was the one selected for examination.



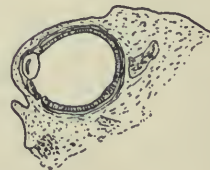
NORMAL 8 day chick embryo.



$\frac{1}{4}$  P.D. with  $\frac{1}{2}$  m.m. filter.



$\frac{1}{2}$  P.D. with  $\frac{1}{2}$  m.m. filter.



$\frac{3}{5}$  P.D. with  $\frac{1}{2}$  m.m. filter.

ectio through the greater diameter of the eyeball of a normal chick embryo at the 8th day for comparison with chick embryos at a similar age which have been subjected to the influence of X-rays.

The surface ectoderm is recognisable as a distinct layer although nuclei and cell outlines are indistinct; this applies also to the epithelium of the alimentary and respiratory tracts.

The epithelium of the optic vesicles and retina are differentiated and not separated, as in the previous cases, from the underlying tissues, and there is also a further differentiation of the cell elements of the mesenchyme. Although



8 days, 22 mm.  $\times 5$ . Control.



8 days, 16 mm.  $\times 5$ .  $\frac{1}{4}$  P.D.  
1 mm. filter



8 days, 11 mm.  $\times 5$ .  $\frac{1}{3}$  P.D.  
2 mm. filter.



8 days, 13 mm.  $\times 5$ .  $\frac{1}{2}$  P.D. 1 mm. filter.

the embryo is less than half the size of a normal 8 day chick embryo, the optic vesicle and lens are only one quarter of the normal size, and there seems to be considerable difference in the relative sizes of other individual organs, such as the kidney and lungs. In the case of the eye the differentiation of the various layers of the retina is not nearly so advanced as in the normal condition. The differentiation of the sclerotic cartilage of the orbit has not taken place, while the iris and ciliary body are not differentiated from the sensitive part of the retina. The pigment of the ensheathing layer of the optic cup is present but the granules are neither so numerous nor so dark as in a normal 8 day chick embryo. There is no indication of penetration of the rods and cones through the external limiting membrane of the retina.

As regards the other organs individual parts are all easily distinguished.

The cardio-vascular system appears normal as are also the amnion, the wall of the yolk sac and the allantois. There is no sign of the development of feathers.

*Series 2 (b).* Daily dose,  $\frac{4}{5}$  P.D. through 1 mm. filter for 8 days.

Of the three eggs in this series one was undeveloped, one was dead, while the third was alive; serial sections were made of the two latter specimens.

(1) The dead specimen had attained the length of 10 mm.; the tissues were macerated and the epithelium was for the most part separated from the underlying tissues. The central nervous system showed folding and in places was disintegrated. Death must have taken place at the commencement of the fifth day.

(2) The living specimen was about half the size of a normal 8 day chick and measured 10 mm. in its greatest length. The surface epithelium forms a distinct layer and is not separated from the underlying tissues. The cell outlines are indistinct and the nuclei are not deeply stained. The epithelial tissues are differentiated in the central nervous system, alimentary and respiratory tracts, as are also the mesothelium of the genito-urinary organs and coelom, and the endothelial lining of the blood vessels. The blood corpuscles are well formed and their nuclei well stained. The optic vesicle and lens show the same degree of development and differentiation as are present in the specimen in *Series 2 (a)* ( $\frac{4}{5}$  P.D.  $\frac{1}{2}$  mm.). No indication of the growth of feathers is present.

*Series 2 (c).* Daily dose,  $\frac{4}{5}$  P.D. through 2 mm. aluminium filter for 8 days.

Of the three eggs one was undeveloped, one was dead (it corresponded to a 72 hour chick), while the third was living and had attained the length of 12 mm.

The surface epithelium forms a distinct layer in which the cell outlines can be distinguished. The structure of the central nervous system is highly differentiated as is also the epithelium of the respiratory, alimentary and genito-urinary systems. The development of the cardio-vascular and other systems has reached that of an 8 day chick embryo, although the size is only that of a 5 day embryo.

The genital gland, although of the same size as that of a  $5\frac{1}{2}$  day embryo, can already be recognised as an ovary. No follicles of feathers are present.



Series 3.  $\frac{1}{2}$  P.D. daily for 8 days.

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(a) $\frac{1}{2}$ mm. filter	(b) 1 mm. filter	(c) 2 mm. filter
(1) Living and measured 13 mm.	(1) Living and measured 13 mm.	(1) Undeveloped
(2) " "	(2) " "	(2) Living and measured 13 mm.
(3) " "	(3) " "	(3) " "

Series 3 (a). Daily dose,  $\frac{1}{2}$  P.D. through  $\frac{1}{2}$  mm. aluminium filter for 8 days.

All three embryos were alive in this series of which one only was sectioned; it had attained the length of 13 mm.

This embryo had reached the stage of an 8 day chick although it had only attained the size of one of the sixth day.

The surface epithelium is a distinct layer, its microscopical appearance is good and cell outlines can be distinguished easily. The histology of the central nervous system is good and highly differentiated. In the optic vesicle the outer extremities of the rods and cones are not seen to be projecting through the external limiting membrane as they do in the normal condition at this age. Pigment is present in the outer pigment layer of the retina. The epithelium of the cardio-vascular, alimentary, respiratory and genito-urinary tracts is normal.

No indication of follicles of feathers is present.

Series 3 (b). Daily dose,  $\frac{1}{2}$  P.D. through 1 mm. aluminium filter for 8 days.

All the three embryos were alive in this series of which only one was sectioned. This embryo had attained the development of an 8 day chick, but only measured 13 mm. in its greatest length. The histological appearances were identical with those of the preceding specimen.

Series 3 (c). Daily dose,  $\frac{1}{2}$  P.D. through 2 mm. aluminium filter for 8 days.

Of this series one embryo was undeveloped, while the other two had attained the length of 13 mm.

In these specimens the histological differentiation was better marked than in any other of the previous specimens, the cell outlines being more clearly marked and the nuclei more distinct.

With regard to the central nervous system; in the pigment layer of the retina, granules could be distinguished, otherwise the specimens presented much the same appearances as in Series 4 (a) ( $\frac{1}{4}$  P.D.  $\frac{1}{2}$  mm.).

Series 4.  $\frac{1}{4}$  P.D. daily for 8 days.

(Average greatest length of normal 8 day chick embryo = 22 mm.)

(a) $\frac{1}{2}$ mm. filter	(b) 1 mm. filter	(c) 2 mm. filter
(1) Not fertilised	(1) Living and measured 15 mm.	(1) Not fertilised
(2) Living and measured 15 mm.	(2) " "	(2) Living and measured 15 mm.
(3) " "	(3) " "	(3) " "

Series 4 (a). Daily dose,  $\frac{1}{4}$  P.D. through  $\frac{1}{2}$  mm. aluminium filter for 8 days.

In this series one egg was found to be unfertilised; in the remaining two the embryos were alive and had attained the length of 15 mm. The histology

was good and the cell outlines and nuclei showed clearer differentiation than in any of the preceding specimens. There was a definite indication of developing feathers on the dorsal aspect of the embryo. This is the first embryo which showed any indication of developing feathers. Although the specimen was dwarfed it exhibited no other deviation from the normal type.

*Series 4 (b).* Daily dose,  $\frac{1}{4}$  P.D. through 1 mm. aluminium filter for 8 days.

In this series all embryos were alive and measured 15 mm. in greatest length.

As regards both size, histology and development these specimens presented appearances identical with those seen in Series 4 (a)  $\frac{1}{4}$  P.D.  $\frac{1}{2}$  mm.

*Series 4 (c).* Daily dose,  $\frac{1}{4}$  P.D. through 2 mm. aluminium filter for 8 days.

In this series one of the eggs was found to be unfertilised, the remaining two were alive and measured 15 mm.

The only difference observed between the embryos in this series and those in the two preceding series ( $\frac{1}{4}$  P.D.  $\frac{1}{2}$  mm. and  $\frac{1}{4}$  P.D. 1 mm.) was that the feathers showed a more advanced stage of development, although this was still less than normal.

#### SUMMARY OF RESULTS.

1. The rays were found to have an inhibiting effect in all cases. The greatest length of a normal chick embryo at the eighth day of development was found to be 22 mm.; of the experimental series the maximum lengths obtained were as under:

Series 1 (a) 1 P.D.  $\frac{1}{2}$  mm. filter = 4 mm.

„ 1 (b) 1 „ 1 „ „	= 4 „
„ 1 (c) 1 „ 2 „ „	= 4 „
„ 2 (a) $\frac{1}{4}$ „ $\frac{1}{2}$ „ „	= 8 „
„ 2 (b) $\frac{1}{4}$ „ 1 „ „	= 10 „
„ 2 (c) $\frac{1}{4}$ „ 2 „ „	= 12 „
„ 3 (a) $\frac{1}{2}$ „ $\frac{1}{2}$ „ „	= 13 „
„ 3 (b) $\frac{1}{2}$ „ 1 „ „	= 13 „
„ 3 (c) $\frac{1}{2}$ „ 2 „ „	= 13 „
„ 4 (a) $\frac{1}{4}$ „ $\frac{1}{2}$ „ „	= 15 „
„ 4 (b) $\frac{1}{4}$ „ 1 „ „	= 15 „
„ 4 (c) $\frac{1}{4}$ „ 2 „ „	= 15 „

2. From the above it is seen that with the exception of the second series the screening had little effect on the total growth of the embryos.

3. The tissues most affected by radiations were the surface ectoderm; feathers were not seen in any of the series except in Series 4; here it was noticed that when using a 2 mm. aluminium filter, they had attained further degree of development than in those protected by a 1 mm. filter; these again were slightly more advanced than those only protected by the  $\frac{1}{2}$  mm. filter.

4. *The central nervous system and eye.* Throughout the whole of the first series (1 P.D.) the central nervous system and eye showed such a degree of disintegration, partly perhaps due to post-mortem changes, that any deductions were impossible. It was noticed that the ill differentiated epithelium of the optic vesicle and that of the retina were separated from the subjacent tissues.

In the second series ( $\frac{2}{3}$  P.D.) it was noticed that the epithelium of the optic vesicles and retina was differentiated and not separated from the underlying tissues. As regards the retina the differentiation of its various layers is not very advanced.

In the third series ( $\frac{1}{2}$  P.D.) the histology of the central nervous system was good and highly differentiated and pigment could be seen in the outer pigment layer of the retina.

In the fourth series ( $\frac{1}{4}$  P.D.) the central nervous system and retina had attained the degree of differentiation of a normal 8 day chick embryo but they were smaller in size.

5. *The cardio-vascular system.* In Series 1 (1 P.D.) the first signs of blood corpuscles were first noticed in the specimen which had been protected by a 2 mm. screen; the heart was formed, but its tissues disintegrated in all members of this series.

In Series 2 ( $\frac{2}{3}$  P.D.) and subsequent series up to  $\frac{1}{4}$  P.D. the heart and blood vessels appeared normal except for diminution in size.

#### GENERAL CONCLUSIONS

In chick embryos irradiated immediately before incubation and then subjected to daily irradiations for several days the following results were obtained. The action of the rays was, as said, in all cases inhibitory, irradiated embryos being invariably smaller than controls. *Within the limit of radiation investigated*, the effects seem rather to depend upon the total amount of radiation reaching the embryo than upon its quality or "hardness." In the series which received a full pastille dose six out of nine specimens examined showed no sign of development at all.

As regards the susceptibility of individual tissues and structures to these conditions, this was found to be most marked in the surface ectoderm, the central nervous system and the eye.

Further experiments have yielded results which indicate that exposure of embryos which have been allowed to incubate normally for a period of 90 hours and which have then been exposed to X-rays for three successive days produces in some cases a certain degree of stimulation as indicated by a slight increase in size. The authors hope to give a detailed description of these experiments in a subsequent paper.

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# ABNORMAL LEFT CORONARY ARTERY OF OX HEART COMMUNICATING DIRECTLY WITH THE CAVITY OF THE LEFT VENTRICLE NEAR THE APEX

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**A** HITHERTO undescribed abnormality was observed in an ox heart received by the above department about the end of October, 1921. Externally, the heart showed at the apex of the left ventricle a circular cyst-like structure. The heart was then held, with the cut end of the aorta pointing upwards, under a tap of running water. The water was allowed to run gently into the aorta, and the cyst-like structure was observed to bulge with fluid. On closer examination, a tubular vessel of arterial type about the calibre of one's middle finger was observed in the interventricular groove between the aorta and this structure at the apex of the left ventricle. This vessel appeared to follow the usual course of the descending branch of the left coronary artery towards the apex of the heart. It should be noted that, anteriorly, over the cyst-like dilatation, the ventricular muscle was quite deficient, and seemed to have been displaced by this abnormal structure.

Heart: weight with attachments of great vessels and fat, 95 ounces.

[Weight of another normal ox heart, 89 ounces.]

Length of heart, 24 cm.)	} during rigor.
Width of heart, 19 cm.)	

The auricles looked normal. The thickness of the walls of the left ventricle during rigor was about 5 cm. and did not differ materially from that of the normal ox heart.

With regard to the previous history and health of the animal, the following facts were obtained:

Age, rising 3 years old. Never off feed; very good feeder; always active; walked to sale from the farm ( $\frac{3}{4}$  mile). Proportion of beef to live weight, fair average.

The calibre and thickness of the walls of the following vessels are given for the purpose of comparison:

Vessel	Calibre	Thickness of wall
Aorta (about 8 cm. beyond the valves) ...	3.0 cm.	8 mm.
Innominate artery (at its origin) ...	1.75 "	5 "
Abnormal artery (at its origin above the cusp) ...	1.5 "	1.5 "

It will be observed that, while the calibres of the innominate artery and abnormal artery are approximately equal, the wall of the latter is much thinner than that of the former.

Further dissection showed that this abnormal vessel arose about 1.25 cm. above the middle of the left posterior cusp of the aortic valve. The tip of the middle finger could be inserted into the vessel at its origin. A coronary artery, smaller in size, arose above the anterior cusp, but no artery arose above the right posterior cusp. In the normal ox heart the calibres of the two coronaries differ considerably, the left being the larger, but the normal left coronary artery did not admit the tip of the middle finger.

No other abnormal opening was noted at the base of the aorta. The aortic wall was healthy and the aortic valves appeared healthy, and, when tested by means of a stream of water directed into the cut end of the aorta, proved competent.

The abnormal vessel passed forward between the left auricular appendix and the pulmonary artery. The first branch came off the main vessel about 3.5 cm. from the cusp, and ran transversely outwards in the left auriculo-ventricular groove. Its calibre appeared similar to that of the normal right coronary artery. This branch was evidently the transverse branch of the left coronary artery and was of normal size.

The abnormal vessel passed along the interventricular septum giving off numerous small branches to the septum without any marked diminution in calibre until it reached just above the apex of the left ventricle anteriorly where it dilated into a cyst-like structure roughly conical in shape with its base anterior and its apex on a level with the inner surface of the left ventricle. With regard to the dimensions of the above structure, the diameter of the base of the cone was about 7 cm. while the height of the cone was about 6 cm. It will be noted that the height of this structure is practically equal to the thickness of the wall of the left ventricle.

The wall of the cone-shaped structure appeared similar in structure to the wall of the abnormal vessel but slightly thinner. It was lined by smooth endothelium, and its base was quite uncovered by cardiac muscular fibres, being apparently in direct relationship with the pericardium. The rest of the wall of the cone-shaped structure was attached firmly to the muscle of the left ventricle throughout its entire thickness.

The walls of the abnormal vessel and the dilated portion were apparently continuous. Anteriorly, where the wall of the dilated portion was not attached to the wall of the ventricle, the epicardium passed directly on to the wall of the dilated portion. At first, the union was not firm, the two being held together by loose tissue, but at a distance of about 2 cm. from the place where the ventricular muscle became deficient the wall of the dilated portion and the epicardium became fused apparently into one.

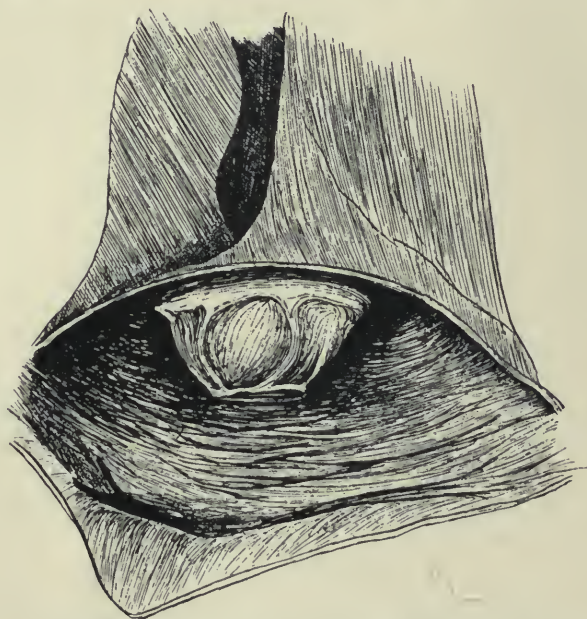
The cavity communicated directly with the left ventricle near its apex by a circular aperture, which was sufficiently large to admit the middle finger, and was guarded by a valve-like structure. Examination showed that the latter consisted of:

(1) an inner fibrous ring, diameter 1.5 cm., forming the circumference of the aperture,

(2) an outer fibrous ring, 3.5 cm. in diameter,

(3) thin fibrous material covered by smooth endothelium, stretching between the two rings and thickened by six or seven fibrous bands running radially between the two circular fibrous rings.

No other abnormality, developmental or acquired, was noted in the right or left chambers of the heart. The interventricular septum did not appear to be in any way abnormal, and the coronary veins both right and left were small. They did not appear to be enlarged on either side of the heart.



Lateral view of valve-like structure between cavity of left ventricle above and cyst-like dilatation below.

From its origin and course, this abnormal vessel was taken to be a left coronary artery—the abnormality affecting more particularly the descending branch of the left coronary artery. The dilatation of the terminal portion of the vessel at the apex was difficult to explain. This dilatation might have been due wholly to the developmental abnormality, or it might have been acquired mainly. If the latter supposition was correct, the dilatation would have been of the nature of an aneurismal dilatation. Support might be lent to this view by the fact that, when the dilated portion was distended with water, it was noted that at two or three places the wall was much thinned. The distension might have been brought about by the escape of blood from the left ventricle throughout the greater part of systole before the opening between the cavities of the left ventricle and the dilated part was closed by the contraction of the left ventricle towards the end of systole.

Developmentally, no explanation of the abnormal coronary and communication with the left ventricle has been suggested.



The only related case on record was described by Mr H. Blakeway in the *Journal of Anatomy*, vol. LII, p. 354. The heart in this case—a child which lived 36 hours—had amongst other abnormalities no direct communication between the left ventricle and the aorta, but an indirect one by means of the anterior interventricular branch of the left coronary artery. Mr Blakeway considered the question of the possibility of the origin of the abnormal communication between the aorta and the left ventricle as being due to some developmental peculiarity of the bulbus cordis. He, however, rejected this consideration.

The actual course taken by the blood in the abnormal ox heart forms an interesting speculation. Before the heart went into rigor, the left ventricle was artificially compressed above the apex to imitate systole, and at the same time a stream of fluid under pressure was directed against the pseudo-valvular opening by means of a tube introduced through the aorta past the aortic valves. Practically no fluid escaped into the dilated part. Again, fluid was allowed to run into the aorta. The aortic valve being competent, most of the fluid passed along the abnormal channel. The fluid entered the cavity of the left ventricle (the left ventricle being empty) through the pseudo-valvular opening, if the left ventricle was not compressed.

It would appear that during the greater part of systole leakage took place directly from the left ventricle to the dilatation at the apex. In all probability, the opening between the left ventricle and the dilated portion would not be closed by ventricular contraction except towards the end of systole. During diastole, unless the pseudo-valvular structure acted as an efficient valve, there must have been free communication between the aorta and the interior of the left ventricle, and the diastolic pressure in the abnormal vessel and in the interior of the left ventricle must have been equal to the pressure in the aorta. After the wall of the distended part at the apex of the left ventricle was laid open, a strong stream of fluid was directed against the valve-like structure. It appeared to act as an efficient valve except when the left ventricle was distended or relaxed.

As bearing on the accepted relation between increased diastolic intraventricular pressure and dilatation and the striking development of dilatation and hypertrophy in aortic regurgitation in man, it is noteworthy that in this ox regurgitation into the left ventricle with its concomitant high diastolic pressure was not associated with appreciable dilatation or hypertrophy.

The following notes give a brief account of the microscopical appearance of the parts of which sections were made:

(1) *Ventricle (left).*

Muscle, healthy. Nothing abnormal noted.

(2) *Innominate artery.*

Intima, healthy.

Media, towards inner part of media regularly arranged bundles of plain

muscle circularly disposed and elastic fibres; towards outer part of media, amongst the circularly disposed plain muscle and elastic fibres irregularly arranged groups of plain muscle, many running longitudinally.

(3) *Wall of abnormal coronary artery.*

Endothelium, healthy.

Subendothelial elastic layer, quite well marked. Wall varies in thickness, the thinner parts being at most one-half the thickness of the thicker portions.

*Thicker portions:* large amount of plain muscle arranged in bundles; rather granular looking elastic tissue between the bundles—apparently split longitudinally in places.

*Thinner portions:* much less plain muscle than the preceding; towards the centre of one portion of the media, small oval-shaped area which does not stain well; nuclei stain fairly well but are variable in shape. The elastic tissue apparently shows large coarse granules and it appears to become fragmented transversely into more or less elliptical portions.

*Externa*, well marked.

(4) *Wall of dilated portion of abnormal coronary artery.*

Two layers: (1) External, epicardium;

(2) Internal, part corresponding to wall of the abnormal coronary artery; practically no plain muscle or elastic fibres; rather degenerate-looking connective tissue showing nuclei which stain fairly well, fibrils, and perhaps "ghost-like" elastic fibres.

Interior to the above is a fairly thick endothelial and subendothelial layer showing connective tissue and elastic tissue arranged parallel to the inner surface; nuclei stain well.

Endothelium appears to show proliferation of its cells, the deeper layers of which show signs of organisation.

(5) *Lining of cavity and subjacent myocardium.*

(a) Endothelium, normal; no proliferation.

(b) Subendothelial elastic layer, fairly well marked.

(c) Layer of more or less homogeneous tissue taking up eosin stain, no sign of elastic or muscle fibres.

(d) More or less continuous layer of about  $\frac{1}{3}$ th thickness of (c), consisting of heart muscle fibres and white fibrous connective tissue.

(e) Vascular layer, thinner than (d).

(f) Heart muscle proper.

(6) *Junction of dilated end of abnormal coronary artery with ventricle.*

Epicardium and wall of distended portion can be seen separated by heart muscle; the heart muscle ceases and the epicardium and the wall fuse loosely at first, but firmly within a distance of 2 cm. from the point where the heart muscle ceases; epicardium at the point where the heart muscle ceases becomes much thinned quite abruptly, and continues thin for about a distance of



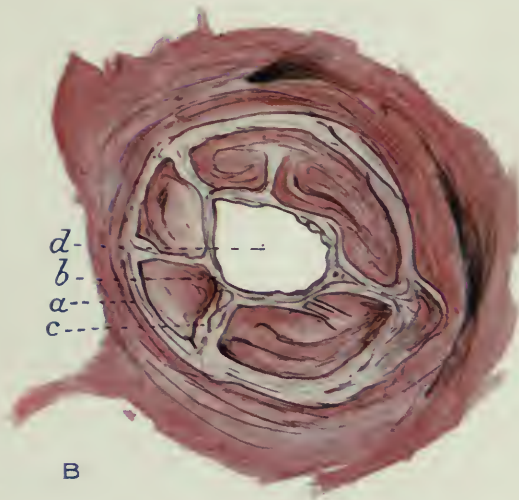


Fig. A. *a, a, a*, track of abnormal descending branch of the left coronary artery; *b*, cyst-like dilatation at apex.

Fig. B. Wall of dilated part at apex has been opened and held back.

Appearance presented by the pseudo-valvular structure on looking at the apex of the heart: (*a*) external fibrous ring; (*b*) internal fibrous ring; (*c*) radial fibrous band; (*d*) communication between the left ventricle and the abnormal coronary.



1.5 cm. as it lies in direct relationship with the wall of the dilated portion; it then becomes thicker, approximating to its original size.

(7) *Branch of abnormal coronary artery.*

Healthy arterial wall.

(8) *Branch of right coronary artery.*

Nothing abnormal to be noted.

(9) and (10) *Coronary arteries from normal ox heart.*

Left: the larger vessel; wall of left varies in thickness considerably.

*Conclusions in regard to:*

I. Course taken by blood during life in the abnormal vessel.

(1) *During systole.* Probably regurgitation occurred from the left ventricle throughout the greater part of systole through the abnormal communication at the apex. This would give rise to a pulse wave apart from the question of the quantity of blood regurgitated. Another pulse wave would be sent along the abnormal vessel from the aorta. In this way the abnormal vessel would be subjected to strain, and the cyst-like part would be subjected probably to the greatest strain. The movement of blood in the abnormal vessel would perhaps be from the apex of the left ventricle towards the aorta.

(2) *During diastole.* The blood-flow in the abnormal vessel would in all likelihood be from the aorta to the left ventricle. The diastolic pressure in the left ventricle and in the abnormal coronary would be high, viz. aortic pressure. Hence conditions would be favourable for increased strain on the abnormal vessel and dilated part during diastole and on the dilated part more particularly during diastole. On the whole, there would be a relative stagnation of blood in the abnormal vessel.

II. Respective proportions of the abnormality, congenital and acquired.

It would appear clear that the communication between the left ventricle and the coronary was developmental wholly. The pseudo-valvular structure must have been present before birth as a congenital peculiarity.

That the abnormal coronary and dilated portion were subjected to abnormal pressures and in consequence became expanded is concluded from the following:

(1) Varying thickness of the wall of the abnormal coronary and dilated part.

(2) The wall does not show the typical structure of a normal artery.

(3) Irregular arrangement of bundles of unstriped muscle etc. in wall.

(4) Evidence of impaired nutrition of portions of the wall of the abnormal vessel.

(5) High diastolic pressure.

In all probability, had the animal not been killed, it would have died at some period of rupture into the pericardial sac through one of the thinned portions of the wall of the dilated portion at the apex.

I am indebted to Professor J. A. MacWilliam for his help and permission to publish the above, and to Mr George C. Kelly for the sketches.

# THE EARLY FORMATIONS OF THE MIDDLE EAR AND EUSTACHIAN TUBE: A CRITICISM

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HÜSCHKE, to whom we owe the description of the auditory vesicle as a structure derived from the surface layer, was also the first to refer the origin of the tube and tympanum to the mandibular cleft or groove. This view, advanced in 1827 and subsequently, met with very general acceptance by anatomists of the time, and has been more or less prominent since then. It is true that certain doubters have arisen at intervals who denied its truth, altogether or in part: for example, Hunt (1876) working on the pig, came to the conclusion that the region arises from an "invagination" of the pharyngeal mucous membrane, and Urbantschitch (1877) also held that the tube and tympanum were formed by lateral outgrowth which had nothing to do with the first groove, while Kölliker and Moldenhauer (1877) do not appear to have looked on the parts as directly derived from the cleft by modification, but rather from an outgrowth associated with it. Piersol (1888) and Siebenmann (1894) also, with a few others, had views which were not quite in line with the accepted one. However, in spite of defections, the formation of the tubo-tympanic cavity from the first pharyngeal groove has generally retained its hold on anatomists as the orthodox description, and, since 1902, the detailed account on these lines given by Hammar (*Archiv. f. mikr. Anat.* v, 59) has been taken as the standard on which descriptions are based and to which references are made in the text-books and other works dealing with the matter.

In 1910 I first described these parts (*B.M.J.*) as made from the "tubo-tympanic recess" of the pharynx, a recess which has its floor formed by the first two visceral arches, while the third arch makes its posterior boundary. A few years later I gave (*J.A.P.* vol. XLVIII) a fuller description, with special reconstructions, etc., amplifying the former more general one. As this description has been adopted in some of our principal text-books, and as it differs in certain fundamental conceptions from the more widely held views of Hammar, it seems necessary to point out<sup>1</sup> where, in my opinion, the earlier representation is open to criticism.

It will be well to confine ourselves, in this matter, practically to the fundamental differences between the two views, and so to avoid a lengthy consideration. The view which I advocate is, shortly, that the tubo-tympanic recess

<sup>1</sup> This was written in 1915. The paper was never finished, however, owing to war work. I have not finished it, as I intended, by some comparative observations, but have confined myself simply to the difference of view in human development.



is a part of the pharyngeal cavity, situated as already indicated, and that it is nearly completely separated from the main cavity by a forward growth derived from the *third* arch, which comes into contact finally with the first arch in the front wall of the recess, so that only a narrow tubal passage is left above the place where they meet. This closing in of the recess from behind only affects its inner part, the outer portion still remaining as the tympanum, thus only communicating with the pharynx by the narrow unclosed front or tubal part of the recess; the tympanum, coming into existence in this way, has in its floor the outer end of the second arch and its groove, in front of this the first groove and arch, while its inner wall is necessarily made by the forward growth from the third arch. Detailed descriptions and accounts of the models can be found in my earlier papers.

There is no essential difference between the two descriptions so far as concerns the separation of the tympanic region from the pharynx by a forward growth, but the origin of this forward growth is referred by Hammar to the *second* arch, and here comes in the fundamental difference. His account of necessity carries the second pouch backwards and inwards, and leaves it on the pharyngeal side of the forward growth, whereas mine leaves it undisturbed in the tympanum, because the forward growth arises on its aboral side. This brief account of the main questions at issue will serve to show the limits of the criticisms I desire to bring forward, and to indicate at the same time the inter-relations of the points with which we are dealing. I propose to show (*a*) that the conditions necessary for Hammar's conception do not in fact exist, (*b*) that those requisite for the view I advocate are present, and (*c*) that the conditions actually found in sections are consonant with and only explicable by the explanation I adduce, and in themselves disprove the other description.

(*a*) If Professor Hammar's view is correct, and the tympanum is separated from the general cavity of the pharynx by tissues derived from the second arch growing forward between the two, it would seem evident that we ought to find indications of that growth and of its effect on the neighbouring structures. The arch is placed below the floor of the recess (figs. 1 and 2) immediately in front of its posterior external angle, which is made by the dorsal portion of the 2nd lateral pouch.

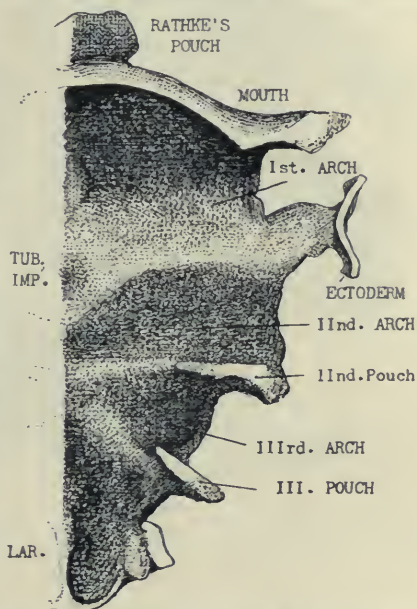


Fig. 1. Ventral surface of left half of pharynx, 7 mm. Shows early stage of recess, with 2nd arch completely in floor. Ectoderm left in contact with 1st pouch; on other pouches the extent of contact with ectoderm is shown by lighter areas.

If the arch thicken, its area as represented in the floor must increase, for if it is going to affect the cavity by enlargement, this enlargement must be in close relation to the cavity. But it does not enlarge: on the contrary, its area becomes smaller, and no condensation is visible within it. Its skeletal bar is close to the lining membrane of the floor of the recess when it first becomes recognisable, and it retains this situation throughout, *except when and where the mass of the forward growth comes in between it and the floor*. It

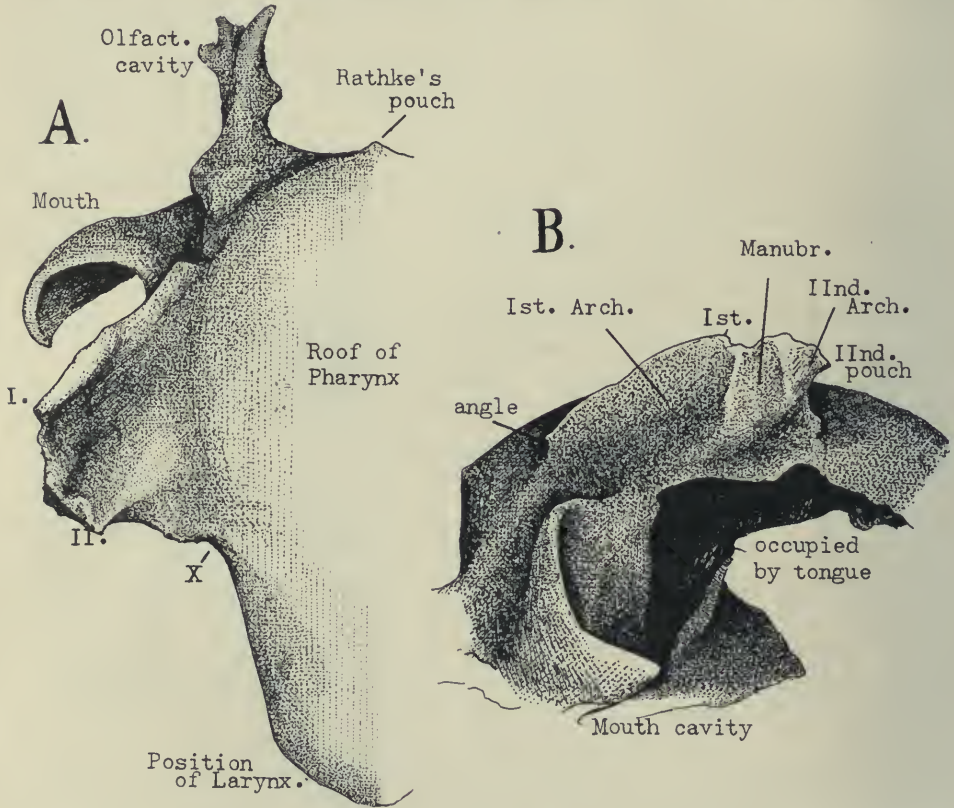


Fig. 2. Pharynx, 16 mm. A, dorsal aspect of recess; I and II, 1st and 2nd pouches; B, view from outside, below, and behind, showing area of manubrial invasion, uninvaded remnant of 2nd arch, 2nd pouch, and, internal to these, the impression of the forward growth.

might be said that here we have the enlargement for which we are looking, the evidence of the existence of the postulated growth from the 2nd arch. Certainly it is evidence of growth, but not necessarily from the 2nd arch, and certainly not capable of effecting the results claimed for it: leaving the question of its apparent origin out of the argument for the moment, to be dealt with later, it will be found not to fulfil the conditions that are required if it is to be accepted as the desired effective growth from the 2nd arch. For one of these conditions is that it must be effective from the outer and front



side of the pouch, in the neighbourhood of the outer margin of the recess, not from its posterior margin. But this growth, separating Reichert's bar in part from the floor of the recess, only does so under the inner part of that floor, altogether internal to the region of the pouch, and up to the time of completion of the "separation stage" it does not extend appreciably under the outer part of the floor (see fig. 5). Moreover, there is never at any time any sign of growth in the outer or juxta-marginal part of the 2nd arch, or antero-external to the pouch: the bar remains in contact with the floor here as in the earlier stages, and in fact is there still in the adult as the tympano-hyal. There cannot, therefore, be any question of growth in this part of the arch, unless Reichert's bar takes part in it, on its crest, so to speak. It is hardly necessary to say

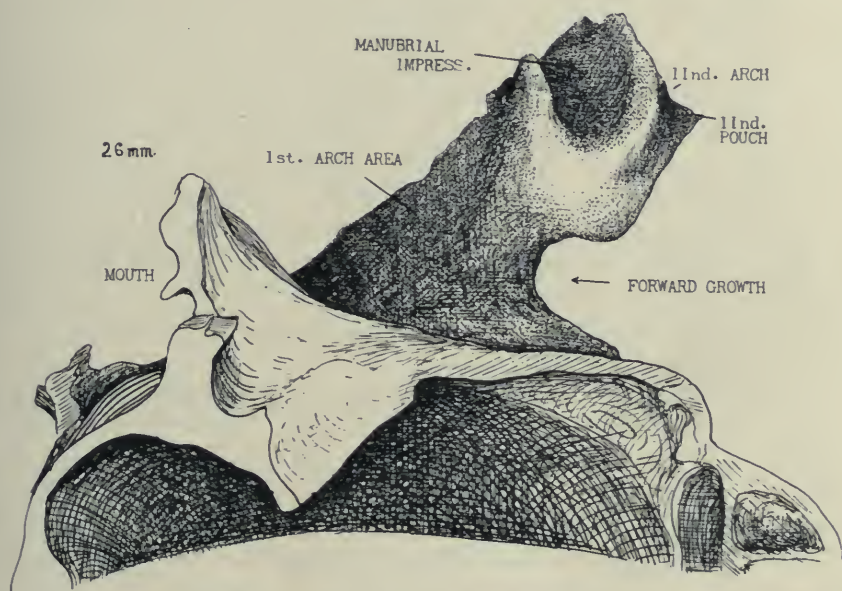


Fig. 3. Pharynx during 8th week from below. To show how the forward growth progresses internal to the 2nd arch area and pouch, next the pharyngeal wall, and is evidently pushing forward from behind

that the bar has nothing to do with the growth, save that this comes in between it and the more internal part of the recess.

I have given drawings in previous papers illustrating the stages of the growth, and I need only now refer to fig. 2 as showing its definite position. The first view is of the recess in a 16 mm. embryo, seen from above: *B* shows the recess laterally from below and slightly from behind. The triangular area labelled as 2nd arch is the part related to Reichert's bar, but the bar is separated from the recess, further in, by the forward growth, which therefore shows in the model as a hollow between the arch area and the pharynx. This impression shows the growth to be wedge-like, with its base behind. Plainly, it does not affect the outer part of the 2nd arch, and cannot displace the

pouch towards the pharynx, and these characteristics remain. In fig. 3, they are as apparent in the 8th week, though by this time the alleged shifting inwards of the pouch ought to have been accomplished and done with long before. We can say, then, that on the one hand there is no growth capable of causing inward displacement of the pouch, and on the other the growth that is present is not only unable to bring about this movement, but, owing to its situation, could only move the pouch outwards—if it were near enough to affect it at all.

When we come to consider the effects of the postulated growth from the 2nd arch we find a similar absence of evidence that effects which would of necessity result from such growth have any existence whatever in fact. A growth of this sort, if it pushes the second pouch medially must do so by pushing it in front of the structures of the third arch, and must then occupy the place, so to speak, of the displaced pouch, and lie between the structures of the 3rd arch and the lining membrane of the tympanic cavity. These seem to be absolutely necessary consequences of such a process, if it occurs, and afford objective tests to which observation can be directed in the embryo.

In this connection the 9th nerve gives us an excellent standard of position in the various stages. The nerve is a particularly useful 3rd arch structure, for it is placed, from the earliest stages of the recess, immediately aboral to the 2nd pouch, being in fact separated by this pouch from the nerve and bar of the 2nd arch. I have illustrated these relations frequently, and they are indicated in some of the outlines given in fig. 4.

Now it can be said at once that nothing, during the formation of the tympanum out of the recess, passes in front of this nerve or separates it from the lining membrane of the cavity, nor does the second pouch change its relation to it, but continues to project in all stages between it and the facial nerve and bar. The later stages shown in figs. 3 and 4 exemplify this, and these conditions and relations between the parts remain until modified in certain minor respects by developments associated with the later growth of the auditory capsule—but this is long after the separation of the tympanum has been effected and completed. The forward growth begins internal to the 9th nerve, that is, on its aboral side, and is plainly evident a considerable time before the period when the 2nd pouch is displaced according to Hammar's description; it can be seen, already definite, in the 16 mm. embryo shown in fig. 2. At this time, then, the growth is altogether internal to the position of the 2nd pouch, situated between it and the pharyngeal wall, and it increases in size in this situation: yet, if we accept the description given by Hammar, the growth which can be seen to be wedging itself in, from behind, between the pharyngeal wall and the pouch, must suddenly and rapidly displace this pouch inwards, that is, it must begin to press on it from its outer side, and push it inwards in despite of the wedge-like mass which has been laboriously forming itself internal to it. Not only is such a reading of the facts almost impossible in itself, but is absolutely negated by the observations which



can be made on any human embryos of the proper stages: the inner wedge is a verifiable reality, the positions of the nerves and the pouch are evident, and evidently constant, but there is not the slightest hint of any lateral or antero-lateral pressure on the pouch, or of any shifting of it in front of the 9th nerve, or of any separation of this nerve from its relation to the tympanic cavity by a lateral or antero-lateral growth or in any way whatever. I have given figures showing their relations and conditions in previous papers, where they can be seen if desired, but fig. 4 gives a series of small outlines of some

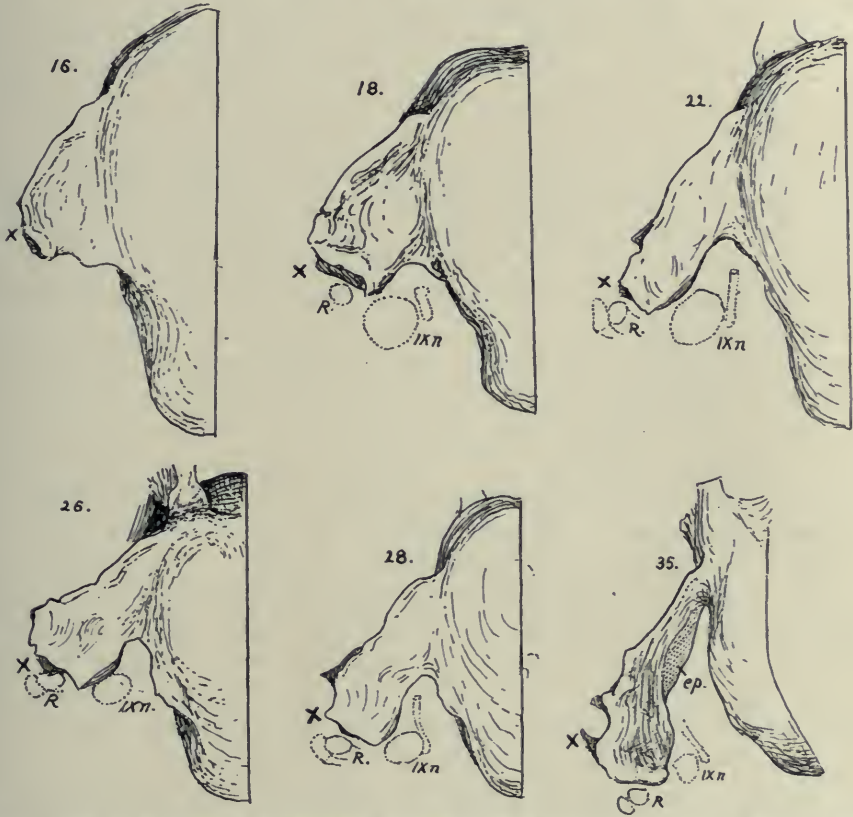


Fig. 4. Dorsal views of stages of separation of recess from pharynx from behind. Embryo lengths are given above each outline. *R.*, Reichert's bar; *X*, posterior limit of manubrial invasion; *ep.*, epithelial lamina below tubal part.

of the models I have made of this region, and in those in which the nerves are indicated it can be seen that their essential positions with regard to the cavity and second pouch remain unchanged, as does the pouch itself, placed between them.

It is to be regretted that Professor Hammar did not include among his figures illustrations of the ventral aspect of the various stages which he modelled. I confess that I find his accounts of these aspects difficult to follow, but I suppose that his models were very much the same as mine of similar stages,

and for this reason regret the omission of figures, for the ventral aspect is a very interesting and suggestive one where the position and extension of the forward growth are concerned. The floor of the recess, seen from within, such as I have described and figured in this journal (1913), gives a demonstration of these matters perhaps even more striking, at any rate to the observer who is not accustomed to dealing with models of cavities.

We come now to what is, if I am not mistaken, the only direct evidence brought forward in support of Professor Hammar's contention that the 2nd pouch is displaced inwards to the pharyngeal wall. It is the description given by him of the conditions in an embryo of 18.5 mm. (N.S.) length, with an illustration of the model: the drawing is reproduced in Keibel and Mall (text-book) where it can be seen by those who cannot consult the original monograph.

The measurements given by Hammar cannot be compared directly with those given in the references to my specimens, for he uses N.S. length, whereas mine are given in greatest total length. I imagine that his 18 mm. stage would correspond more or less with a "greatest length" of about 22 mm.

I may confess at once that the figure is to me the illustration of some condition quite abnormal: one may make guesses about the nature of the abnormality, but I have no doubt in my own mind as to its existence. I have examined every embryo which I could find sectioned, between 18 and 30 mm., and have found nothing whatever to suggest a remote resemblance to the curious appearance presented by this specimen. This merely negative evidence would not, of course, be of very much weight in itself, and I would have had very great hesitation in stating my belief—however strongly I might hold it—that the specimen is not normal, if that belief did not receive such strong indirect support from these negative observations. For all my specimens exhibit conditions pointing to an even progress of events, such as is illustrated in the series in fig. 4, and among these specimens are embryos of 18, 22, and 25 mm. (not to mention one or two others apparently lying between these limits but of doubtful official measurement). Now these three embryos are all in the line of even progress, as are the 26 mm. and 28 mm., and none show any sign whatever of growth lateral to the 2nd pouch, or of displacement of this pouch: yet somewhere between these stages there is said to occur one in which these things take place, one which therefore starts *de novo*, runs its course, produces its effect, and leaves no sign of its occurrence behind it, and all this while the embryo is increasing in length some 2 or 3 mm. The mere statement of the necessities that follow on the negative observations to which I have referred is enough to indicate the support they render to the opinion formed on the first view of the figure of the model, and, when the existence is remembered of the solid forward growth internal to the pouch, the suggested occurrence would seem impossible. I do not wish to lay stress on the appearance of the "pouch" in this figure, though it is strangely incompatible with the idea of a structure being possibly displaced by solid growth, and I am

content to leave the matter here, pending an explanation of the curious condition which will enable it to occupy its proper place.

The argument, then, against the acceptance of the explanation given of this 18.5 mm. (N.S.) specimen is not founded on its extraordinary appearance, but on the stability of relations between the pouch and the structures on each side of it, and the wall of the recess close to them, and on the impossibility of conceiving the necessary growth appearing and acting and disappearing in the very short intervals existing between the specimens examined. The argument, to my mind, is an effective one, and disposes of any attempt to shift the pouch across to the pharynx, whatever may be the opinion held about the specimen concerned.

This, of course, does not necessarily affect the fact that a remnant of the 2nd pouch is found on the pharyngeal wall. It is more convenient to deal with this later: for the present it is enough to point out that the remnant is there long before the postulated "shifting" is said to occur, so that the theoretical necessity for supposing such a movement as that which we have just been considering does not exist.

(b) Turning to the consideration of the view which I advocate, it is evident that a good deal of what has been said already is applicable positively in its favour. Thus, the forward growth takes place from behind, on the inner or aboral side of the 2nd pouch, i.e. from the area of the 3rd arch: the 2nd pouch remains unaffected, altogether external to, and on the oral side of, the growth: the growing mass pushes the limits of the recess-cavity before it, hence must pass forward over the 2nd arch structures, and so we find it separating the skeletal bar from the recess: but the outer part of the bar still remains in relation with the outer part of the floor of the recess, which becomes a postero-external part of the floor (outer wall) of the tympanum as the separation proceeds. It is unnecessary to dilate further on these matters, for their bearing on the question is quite clear, and I do not think there is any fact whatever, either of direct observation, or of any "necessary effect," which is not in absolute accordance with the view which I have brought forward concerning the nature of the forward growth. As for the particulars, they can be considered with the following section.

(c) *The conditions in the human embryo.* I have previously given full accounts, with figures from models, etc., of the various stages of evolution of the tube and tympanum from the tubo-tympanic recess, so that it is only necessary here to run over the main facts of the stages. In fig. 4 are given miniature reproductions of the outlines of the region concerned as found in the models made from various stages: the series is not complete, but it is unnecessary to put others between those shown. The most important difference between the early and late members of this series is plainly that due to the increasing concavity of the posterior margin of the projection of the tubo-tympanic recess: this margin proceeds at first with an irregular line inwards and rather backwards from the 2nd pouch to the pharyngeal wall. There



quickly comes a forward bowing of the line, growing into a marked and deep forward convexity, particularly noticeable towards the inner part of the margin, and this progresses until only a constricted tubal portion is left connecting the pharynx and the tympanum. This concavity is produced by the forward growth which we have been discussing. The area of the second arch is seen on the lower aspect at 7 mm. in fig. 1. It is invaded later from in front by a manubrial extension from the 1st arch, and only a small portion of its territory remains uninvaded, namely the posterior part, covering Reichert's bar and just in front of the 2nd pouch. The 2nd pouch can be seen from the dorsal side as an angular projection in all the stages shown in fig. 4. The manubrial invasion, the position of which within the area of the 2nd arch is described by Hammar, is marked behind by the little secondary point *X* in the outlines, so that the remaining unchanged part of the 2nd arch is easily placed between this and the blunt angle of the 2nd pouch.

If we come now to consider the genesis of the forward growth which determines the general arrangement of the regions, it would seem clear that it can only be one of two things. The shape of a cavity, such as that of the pharynx or the tubo-tympanic recess, depends on the structures that form its walls, and we cannot imagine that the cavity itself, or its lining layer, possesses the power to alter its form: power of growth exists, of course, in certain parts, as in the lateral pouches, but it cannot be claimed for the layer in general, and even in the case of the pouches the direction in which the growth is effective seems to be determined by the surrounding structures. The only structures in relation with the floor of the recess, and determining its form, are the mesodermal pharyngeal arches, and the cavity lies compressed between these and the otic capsule, etc., in relation with its roof. The forward growth begins in the floor region, as can be seen in fig. 2, and hence has an "arch value" in origin, and, as it evidently appears near the hinder part of the recess, the 1st arch can be excluded. The floor growth, as can be seen in figs. 2 and 3, and especially in reconstructions of the recess seen from within, such as I have shown in vol. XLVIII of this journal, is evidently pushing forward from the region of the back wall of the recess, and as it increases in size it begins to push this back wall forward and thus to cause the concavity here as seen in "cast" models, so that the floor growth is a little in advance of the concavity. But the hinder wall of the recess is from the beginning made by the 3rd arch, so that the forward growth must be looked on as derived from this arch, and all its relations and details seem to be consonant with this origin. Some of these have been brought forward earlier in this paper, and others have been dealt with at greater length in previous papers: I need not recapitulate these nor I think lay any further stress on the matter, for it seems to me almost self-evident, and apparent to any unprejudiced eye looking at the reconstructions.

The outer part of the 2nd arch remains undisturbed, with its pouch angle, though the whole region is pivoted round a little so as to face somewhat



differently, but the rest of the arch is separated from the floor of the cavity by the increasing thickness of the forward growth. This can be well seen and appreciated in the reconstructions of the floor (1913) but are shown here (fig. 5) in another way: the drawings are from linear reconstructions made along the line of the hyoid bar, showing its relations with the floor, and exhibit the increasing thickness and results of the new growth passing between the bar and the floor of the recess. Different enlargements are used, to make the sections more or less of the same size. The line of section is not transverse, but would meet its fellow of the opposite side at a wide angle, being directed

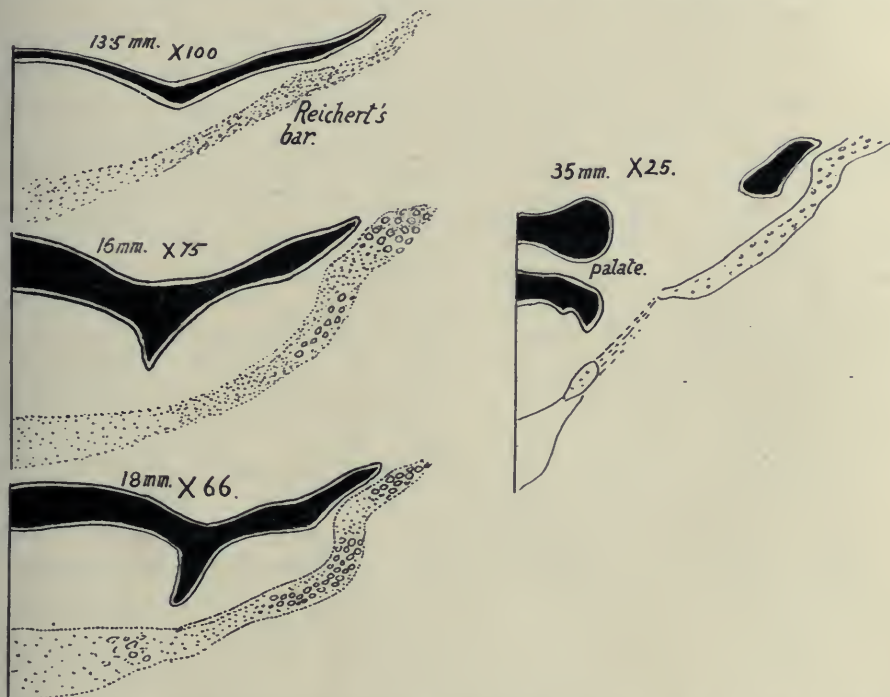


Fig. 5. Reconstruction sections across pharynx in the line of Reichert's bar. To show increasing distance between bar and inner part of recess due to forward growth. Outer part of bar remains in relation with recess.

rather forward, so that the breaking of continuity between tympanum and pharynx from behind does not appear in the sections till relatively late. The first sections show the increasing depth of the growth, and sinking of the hyoid bar, correlated with increasing height of the pharyngeal cavity (of which the growth is seen to form the outer wall here) while the general level of the recess and of its pharyngeal opening is kept at about its original position with relation to the roof of the pharynx. This relation of the growth from the 3rd arch to the pharyngeal wall gives it the opportunity of sending a process forward to join the (maxillary) palate fold, which process then becomes apparent on the pharyngeal wall as the pharyngeal extension of the palate. I described this

process first in 1910; subsequently Michio Inouyé showed the pharyngeal extension to be a secondary part, joining after its appearance, in moles and mice.

Reconstructions in this line of section through the second month exhibit little additional (save that the palate extension begins to show) and are not reproduced, but at 35 mm. the growth has definitely pushed the hinder border of the recess over the line of the bar: here the survival of the relation between bar and recess is seen in the outer part, while the hinder part of palate fold, which has elongated, comes into the section and illustrates its association with the growth.

The 2nd pouch, the angle seen between the 9th nerve and the nerve and bar of the 2nd arch, remains throughout the series. Hammar, believing that this pouch—which he recognises as such in his earlier specimens—undergoes shifting in his 18.5 mm. (N.S.) stage, naturally does not recognise it in the recess after this: but his reconstructions of later stages show it nevertheless, although it has not been dignified by labelling. I need not repeat what I have said already about the constancy of its relations, but I desire to insist on these as matters of primary importance, for *the pouch cannot move when the structures in front of it and behind it are undisturbed, and when nothing comes between them and the lining of the cavity in relation with them.* Whether the angle is really the dorsal part of the pouch or merely the stump of this part is only of academic interest, but the constancy of relations is practically the important matter, and is enough to ensure that the angle in the later stages is the same thing as that in the earlier ones, with all the consequences which I have endeavoured to show depending on this.

Two more points remain for consideration. The first has to do with the existence of a derivative of the 2nd pouch on the pharyngeal wall, claimed by Hammar to be the displaced structure originally found on the recess. I have never wished to deny the pouch-value of this, for I believe it to be a part of the 2nd pouch, but only to represent its ventral portion: the dorsal portion remains as the angle so frequently mentioned, and the forward growth passes forward between the two. The elongated pouch of a 7 mm. embryo is seen in fig. 1. As the head grows in breadth the outer and dorsal part is drawn out still further, and contact with ectoderm (precervical sinus) becomes confined to the inner part. An embryo of 13.5 mm. shows the drawn out pouch extending along the lower aspect of the short hinder margin of the recess, and from its inner end, definitely on the pharyngeal wall, there is the remnant of the external pharyngeal duct leading down towards the former site of the precervical sinus. A 15 mm. embryo shows the complete pouch, though much less clearly, and even at 16 mm. (fig. 2) there appear to be remnants of it in the irregularities on the posterior margin of the recess: but although the forward growth is breaking up this intermediate part of the pouch, its outer and inner (dorsal and ventral) portions remain unaffected, on the recess and side wall of the pharynx respectively. This short account will show that I differ

from Hammar in that I recognise this pouch-remnant as being there *ab initio*, and it can be found there by anyone who takes the trouble to look for it.

The second point does not directly concern the main object of this paper, but I call attention to it because of its possible bearing on the explanation of certain cysts found immediately below the petrous region—cysts which are put into that heterogeneous collection which clinicians lump together as “branchial,” but which certainly are not branchial if that term were used in its proper sense. The point referred to is the occurrence in the normal development, in the last phases of the “separation stage,” of an epithelial (double) lamina below the short tubal connection between tympanum and pharynx.



Fig. 6. (a) Section, 35 mm. below level of patent tube. *Lam.* epithelial lamina connecting pharynx (*Ph.*) with tympanum (*T*); *M.* Meckel's cartilage; *R.* Reichert's cartilage.  
(b) Schemes to show formation of lamina; explanation in text.

Its extent is seen in the 35 mm. reconstruction in fig. 4 and its appearance on section is shown, with diagrams representing its formation, in fig. 6. The first of these diagrams is a scheme of a section across the inner part of the short recess of an early stage, parallel with the wall of the pharynx: the 3rd arch (horizontal lines) forms the hinder part of the floor and limit of the recess, the 1st arch (*M*) forms its front part, and the 2nd arch (dotted area) is between these two in the floor, separated from them by the 2nd and 1st grooves respectively. In the succeeding schemes the 3rd arch is seen to extend forward under the lining membrane, over the second, obliterating the 2nd



groove in doing so, and gradually pushing in the hinder boundary of this part of the recess. The 2nd arch thus drops out of relation with the recess here.

The forward growth of the 3rd arch goes on, pushing in the back wall still further, but along the floor it is limited in front by the first groove. The result is that the growth applies itself to the surface of the 1st arch; the lower portions of the epithelium, thus pressed together, adhere, and so the epithelial lamina is formed. The tracing of a section from a 35 mm. embryo exhibits this lamina connected on the one hand with the lining membrane of the lower part of the tympanum, and on the other with the lower part of the pharyngeal opening of the tubal part, through both of which parts the section passes.

It is clearly evident that the original 1st groove is represented by the free edge of this lamina (see schemes) and has nothing to do with the formation of the cavity of the tube, which is really a remnant of the old recess cavity, persisting in its most anterior part, immediately below the roof. The tube is more or less parallel with the groove, although this is not quite a true description, but the common statement that it *is* this groove is wrong and misleading in many ways, and ought not to be made by anyone acquainted with the details of its ontogenetic development.

The epithelial lamina, made in this way, does not seem to last very long. It is well marked in my specimens of 35 and 37 mm., it is apparently commencing in a third of ? 32 mm., and there is no sign of it in one of 40 to 42 mm. It seems to be at its best about the 35 or 36 mm. stage. I have not, so far, found any apparent remnants of it in still older specimens, but the possibility of such remnants existing is undeniable and for this reason—as well as from a desire to foster a truer conception of the formation of the tube—I call attention once more to its presence.

This paper has been almost entirely controversial, and hence difficult to summarise. I have endeavoured in it to show that the conditions which *must* be present, if Hammar's description is correct, do not in fact exist; that those which must be present if my description is accurate are in fact there, and the description is founded on them; and that the stages found in the human embryo are only consonant with the explanation I have given of them. This means that the separation of the tympanum from the pharynx is effected by a forward growth from the *third* arch, and not from the *second*, as Hammar maintains, and that the outer part of the 2nd arch, with the dorsal part of its pouch, remains in the tympanum. The ventral part of this pouch is on the pharyngeal wall.

I have also recalled the existence of an epithelial lamina below the developing tube, and have pointed out that the tube cannot be described correctly as a persisting first pharyngeal groove.



# THE DESCRIPTION OF A NEANDERTHALOID AUSTRALIAN SKULL, WITH REMARKS ON THE PRODUCTION OF THE FACIAL CHARACTERISTICS OF AUSTRALIAN SKULLS IN GENERAL

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THE skull which is the chief subject of the following description belongs to the incomplete skeleton of an Australian aboriginal presented by J. R. Glyde, Esq., of Sydney, New South Wales, to the Department of Anatomy, University of Sydney. The skeleton had been exhumed at Tamworth in 1880, and was known to be the remains of "Jenny" an aboriginal female.

The skull exhibits an enormous development of the superciliary ridges and glabella, a comparatively well developed bregmatic eminence and a marked development of the torus occipitalis. Added to these primitive features are an extremely low sloping forehead, and a forward slope of the occipital plane of the os occipitale, so that the maximum occipital point coincides with the inion. These features have been referred to in this place on account of the presence of similar characteristics in Neanderthal skulls, a fact which prompted the present description. In addition the aboriginal crania in the Australian Museum, Sydney, and in the University of Sydney Medical School Collections (1. Museum of Normal and Morbid Anatomy, and 2. Anatomy Department) have been investigated for the purposes of comparison. The general results of this survey are embodied in this paper.

The skull which is specially described in this paper will be referred to under its catalogue number (No. 792, Anatomy Dept. Collection). Where special features of other skulls of this collection are recorded, such skulls are indicated by plain catalogue numbers. Skulls selected from the Museum of Normal and Morbid Anatomy (Medical School) are specially indicated. The Australian Museum skulls include the Roth collection, comprising 90 specimens, which were described by Klaatsch (12). We wish to acknowledge our indebtedness to Klaatsch's work. We have followed his plan of description and tables of measurements of Australian and pre-historic skulls, as a basis of comparison. The Western Australian Skull (B. 10283 Australian Museum) and the South Australian (No. 1719 Stuttgart Museum) referred to in this paper were also described by Klaatsch. When specimens of the Roth series are referred to they will be indicated by their original Roth number. The remaining skulls of the Australian Museum collection are indicated by their catalogue number.

## I. FACIAL SKELETON

(a) *Supraorbital, Nasal and Orbital regions.* The glabella and superciliary ridges of No. 792, which are of coarse texture, reach a degree of development which exceeds that of any other modern skull examined by us. This great development of the superciliary ridges together with an exceedingly low sloping forehead, are the two factors which determine the primitive appearance of the forehead as seen in *Pithecanthropus* and in the Neanderthal specimens

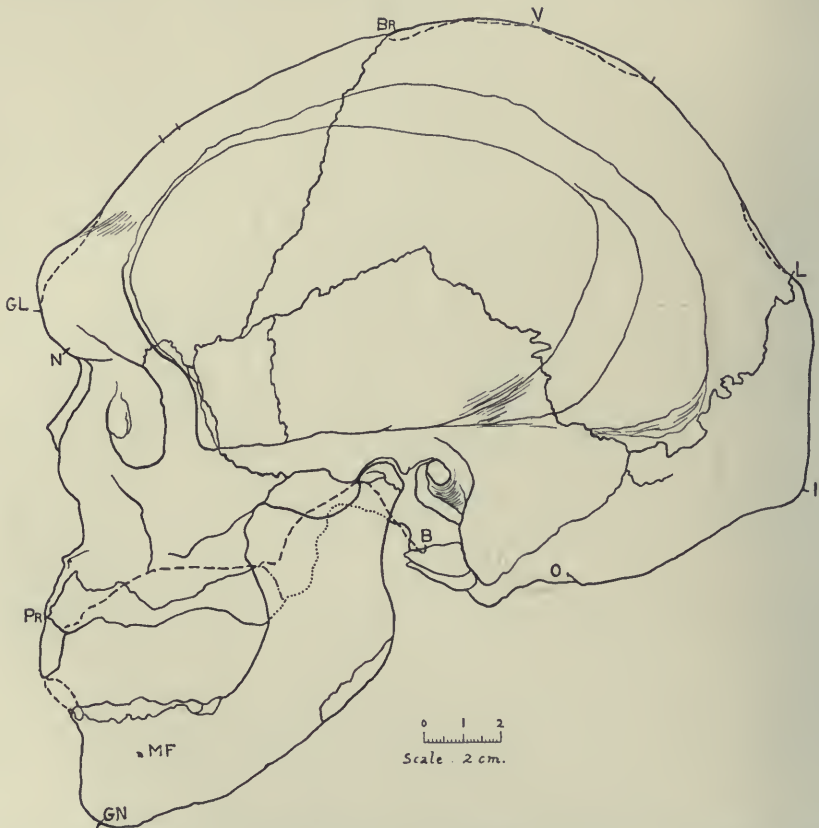


Fig. 1. Norma lateralis of Australian skull (No. 792) (Frankfurt plane). The dotted line indicates the median plane of the skull.

(fig. 1). The projection of the glabella in front of the most depressed portion of the bridge of the nose is 16 mm. This has been measured by making horizontal sections of the skulls with the aid of Lissauer's diagraph (fig. 4). The medial angular process is also well marked, exceeding that of the Kalkadun skull (R. 62), a specimen which Klaatsch remarked upon as presenting an excellent state of development rarely so pronounced amongst Australian aborigines. The vertical height of the superciliary ridges in the region of the supraorbital notch in the Kalkadun skull is 13 mm. whereas in No. 792 this

vertical diameter is 18 mm. (right) and 21 mm. (left). Laterally the vertical extent and prominence of the ridges decrease, but in the region of the external angular process there is an increase in the size of the ridges forming a massive lateral projection. There is therefore present a torus supraorbitalis corresponding to Type III of Cunningham (5) and resembling that present in the Neanderthal specimen. There is a pronounced depression between the supra-orbital ridges as they pass inferiorly to fuse with the glabella—an additional Neanderthal feature. In No. 792 the distance of the deepest point of this depression (facies supraglabellaris) from the nasion is 29 mm.; a comparison with the distance of this point from the bregma (99 mm.) gives an index of 29:29 (Schwalbe's index) which is within modern limits (21–30). The Neanderthal is considerably higher, 43.1 (Klaatsch) and Spy II, 34.4 (Schwalbe).

The absolute measurement with the tape from nasion to ophryon in No. 792 is, however, 43 mm. as compared with 41 mm. in the skull of an Australian aboriginal in the Turner series (xxix. B. 12, Cunningham (5)) and 43 mm. in the Neanderthal cranium. The correspondence of No. 792 to the Neanderthal in this respect emphasises the inadequacy of Schwalbe's index, as mentioned by Klaatsch and Cunningham.

The division of the superciliary ridges into a medial "arcus superciliaris" and a lateral "planum supraorbitale" is practically absent in No. 792. This absence is a primitive feature. The absence of this subdivision in No. 792 is more complete than in the Kalkadun skull, another point of resemblance to the Neanderthal specimen. This serves to emphasise the contention of Cunningham and Klaatsch in opposition to Schwalbe, that the subdivided condition of the superciliary ridges in living races is not a point of distinction from Neanderthal types, which can be applied absolutely, for, as in this instance, an Australian skull has occasionally to be excepted.

Above the tori supraorbitales, the facies supraglabellaris passes laterally into the sulci superciliares; these extend to the temporal crests, over which they pass into the temporal fossae. These sulci are not so pronounced as in the Neanderthal calvarium, but apparently approximate to the N.S.W. and Queensland specimens (xxix. B. 12 and xxix. A. 10 respectively) figured by Cunningham (5). Though shallow, these sulci attain a width of 15 mm. on each side which is less than in the Neanderthal but greater than in the above-mentioned N.S.W. cranium. These sulci look upwards, as well as forwards, a character which obtains to a greater degree in the Neanderthal (fig. 7).

Section of the skull revealed the fact that there was present an unusually large frontal air sinus (fig. 2). Cunningham (5) quotes Logan Turner, who found that by illumination he was able to map out these sinuses only in 20 out of 69 aboriginal skulls, and that it was altogether absent in 30.4 per cent. Relatively small frontal air sinuses close against the inner table of the cranial wall, bounded in front by a thick layer of condensed bone and situated at the base of the torus, are as Cunningham points out, usually to be found in the Australian aboriginal, who in this respect, forms a link with the Neanderthal race and



anthropoids. In No. 792 the condensed outer table of the frontal bone reaches a maximum thickness of 7.5 mm. at the glabella. The sinus on each side extends laterally for 4.3 cm. upwards between the tables of the frontal for 4 cm., and backwards between the two laminae of each orbital plate of the frontal almost to its posterior border. Posteriorly, the inner table of the squama frontalis is only 1–2 mm. in thickness. The maximum interval between the opposed surfaces of the two tables in the mid-line is 18 mm. There is a medial frontal sinus opening into the right infundibulum in addition to the lateral excavations. The extraordinary combination of a large torus and a large

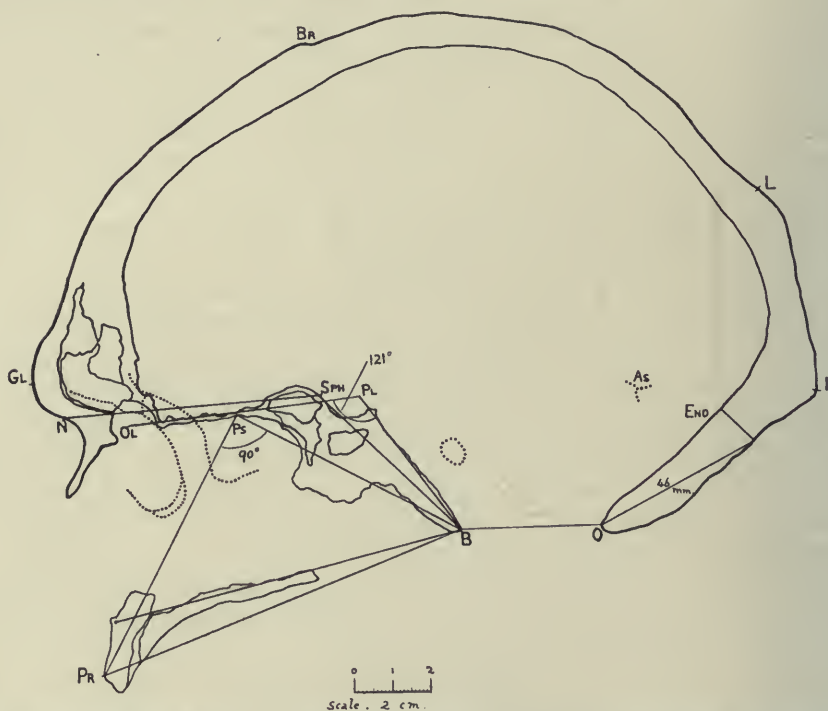


Fig. 2. Median sagittal section of Australian skull (No. 792). The external auditory meatus, the asterion and the margins of the orbit are superposed on dotted outline. *Ol, Pl.* indicates the plane of the cribriform plate.

frontal sinus lead to the result that the supraorbital region of the frontal forms a considerable part of the orbital roof. The greatest length of the precerebral part of the roof of the orbit in the mid-supraorbital region is 25 mm. in No. 792 compared with 20 mm. in the Neanderthal and 16 mm. in the N.S.W. cranium (xxix. B. 1 Turner series) described by Cunningham (5). In this way the size of the frontal lobe is greatly limited. The combination of large tori supra-orbitales and large frontal air sinuses found in No. 792 is, however, apparently very similar to that described by Cunningham (6) in the head of Boco, an aboriginal from South Australia. In this case the glabella was 30 mm. anterior



to the frontal pole of the cerebral hemisphere, compared with 26 mm. in No. 792.

In many respects the nasal region exhibits typical aborigina features to an average degree. Below the well-marked nasion, there is a second depression which corresponds with the upper margin of the projection of the nose in the living state. The nasal bones together present the usual saddle-shaped appearance. The medial borders of these bones which are partly synostosed, project moderately, showing a tendency to bridge formation, more pronounced than in many Australian skulls. On the other hand, No. 795 presents a well-marked bridge without any sign of a nasal depression. In some cases the nasal bones besides being on the whole small, narrow to such an extent superiorly that the frontal processes of the maxillae are separated by only a narrow interval (4 mm. in No. 620). In R. 87 (aboriginal child) the processes meet superiorly behind the nasals.

The lower margin of the apertura piriformis presents the usual aboriginal features. The anterior nasal spine is poorly developed. There is a well-marked fossa praenasalis on each side below. This is limited anteriorly by a crest ("crista praenasalis"), which is continuous with the lateral sharp boundary of the apertura piriformis. Posteriorly this fossa is bounded by a second crest ("margo infranasalis"), which runs laterally towards the commencement of the inferior concha (fig. 6).

In No. 792 the lower limits of these two crests are indistinct, but in B. 10510 (Australian Museum) they converge towards one another and terminate in the spina nasalis anterior. In this way the "crista praenasalis" forms the inferior boundary of the apertura piriformis, and the fossa praenasalis is situated in the floor of the nasal cavity. In the majority of the Roth skulls the crista praenasalis becomes indistinct above the roots of the incisor teeth. Examples of a distinctly bifid anterior nasal spine are seen in Nos. 2355 and 2356 (Medical School Museum). The spine is prolonged into a median crest between the incisors in No. 477 (Medical School Museum).

The outstanding feature of the nasal region is that the skull falls into the leptorrhine class, the nasal index being 47.2. In his Challenger Report, Turner (19) says that all observers agree on the platyrrhine character of Australian skulls. Some are mesorrhine, but the leptorrhine condition is practically unknown, though Turner's authentic Mudgee skull was of this type. Nevertheless, as shown above, certain features, e.g. the well-marked nasal depression, the depressed nasion above this, the narrow nasal bones, poorly marked bridge and the fossa praenasalis, are typically Australian features.

By Cameron's method (4), the naso-orbito-alveolar index was measured on the projection of the norma facialis and this placed the skull in his group III which includes Australian aboriginal, Negro and Melanesian skulls.

The orbit in No. 792 has a shape intermediate between the large approximately circular type and the vertically compressed type.

The infraorbital fossa is an undivided depression. Of the specimens under review, it is exceeded in depth only in a Queensland skull, B. 10510 (Australian Museum), where there is a remarkable excavation undermining the infra-orbital margin.

That part of the zygomatic bone which enters into the formation of the margin of the orbit is not sharp but has a rounded bevelled border. Turner (19, p. 32) says in regard to this point, "the orbits in the males were characterised both by the massiveness of the upper orbital border and by the peculiar breadth and curvature of the malar bone where it formed the outer boundary, which wanted the sharpness one sees in crania generally." Klaatsch also directs attention to this feature for which he offers no explanation. For the following reasons we believe that the rounded character of the inferior orbital margin is due to the large size and great degree of wearing of the molar teeth often to be found in Australian aboriginals:

Firstly, the rounding of the orbital margin is most marked in those skulls with a marked degree of wearing of the teeth. Klaatsch (12, p. 79) refers to R. 16 as showing a degree of wear corresponding to many pre-historic European skulls, and greater than that of any other aboriginal he had examined. In this skull the orbital margin is exceptionally well rounded. A survey of the collections under consideration, proves that this relationship exists in the majority of cases.

Secondly, the bevelled or rounded condition of this border is not found in childhood and is only slightly present in early adult life in the specimens under review. It is apparently acquired therefore in adult life, following the usage of the permanent dentition.

Thirdly, in those skulls in which the teeth were neither massive nor well-worn, the orbital margin was usually sharp; and the zygomatic bone was not massive (e.g. R. 12, R. 49).

We, therefore, conclude that the amount of use of the molar teeth by a given individual, together with the massiveness of the teeth in the Australian aboriginal, contributes to the formation of a rounded orbital margin. There are exceptions to this, however, a sharp orbital margin sometimes being present, together with well-worn teeth. In these cases the masticatory apparatus was less well developed, the palate being usually narrow and the teeth comparatively small (R. 82).

Features associated with this rounding of the margin, are a broadening of the cheek region and a lateral convexity of the zygomatic arch, as mentioned by Turner. This gives rise to the diamond-shaped appearance of the face often observed in the Australian aboriginal (Cunningham (6)).

We consider also that these features are due in part to the operation of mechanical factors. The zygomatic bone is strengthened in order to accommodate the masticatory muscles and to support the force transmitted upwards by the molar teeth during grinding. So marked is the increase in bone formation in the case of R. 2 that a ridge is formed on the zygomatic

bone. It is directed antero-posteriorly so dividing the outer surface of the zygomatic bone into two portions. The upper of these two surfaces is separated from the orbital cavity by a smooth rolled border (the lateral and inferior margin of the orbit). In this case the massive molars are extensively worn.

The zygomatic arch of No. 792 has an upward convexity, while the roots posteriorly form a plate which bears inferiorly an extension of the glenoid fossa. The thickness of this plate is 6 mm. compared with 9-10 mm. in Spy II.

The lower border is irregular being distinctly notched by an impression for the masseter. There is a lateral convexity, the greatest inter-zygomatic diameter being in the temporal segment; this portion of the arch measures 11 mm. vertically and 5 mm. transversely. The strength of the zygomatic arch in the skull of the Australian aboriginal is to be correlated with the racial features exhibited by the facial skeleton.

#### *The Mechanism of Production of the Facial Characteristics of the Australian Aboriginal.*

The zygomatic arch forms a massive support for the masseter muscle while its lateral convexity increases the size of the temporal fossa to accommodate the other muscles of mastication. In addition to accommodating the masticatory muscles, this stout arch forms a buttress of support for the body of the zygomatic bone which receives and transmits the stresses and strains which it receives from the maxilla. Now the teeth of the aboriginal, which are usually massive, have to contend with a molluscan, fibrous and often gritty diet. On account of these factors, the maxilla must be of stouter structure and in consequence a general massiveness results. The molar teeth are mainly supported by the vertical ridge of the maxilla proceeding vertically upwards to the zygomatic process, while the canines and incisors (as in the gorilla) transmit their thrust through the frontal process of this bone. These columns may increase in size to such an extent that the area above the premolars appears hollowed out, i.e., there is formed an infraorbital fossa (R. 2 and R. 24). In other cases this fossa may become deep through an actual excavation. In these cases the roots of the teeth may be divided into two sets as in R. 12. In this specimen the vertical ridge of the maxilla supports the roots of the molar teeth which converge towards it, while the roots of the premolars slope forwards towards the frontal process. When, however, the molar-premolar root arcade is uninterrupted in specimens which exhibit a tendency to squareness of the palate as in R. 10, R. 24, R. 35, R. 39, and R. 69, then the infra-orbital fossa is often absent or very shallow. This is because force is transmitted vertically upwards to the infraorbital margin, between the main pillars of support. These features explain why all grades of development of the infra-orbital fossa are possible in Australian skulls.

In Australian aboriginals, the frontal process is usually stout and powerful. It supports the thrust of the incisors, canines and sometimes the premolars. The two frontal processes often approximate to one another being separated



only by narrow nasal bones. In many Australian skulls they are supported by a relatively large medial angular process.

The molar teeth are supported by the vertical ridge of the maxilla, which transmits the strains received by it to the zygomatic bone. Thereafter the strain is mainly supported by the fronto-sphenoidal process of this bone. From thence it passes to the external angular process of the frontal. The result of this increase of strain, leads, we believe, to increased bone deposition in the vertical ridge of the maxilla in the zygomatic bone, and in the external angular process of the frontal bone. The fronto-sphenoidal process of the zygomatic bone and the external angular process of the frontal bone, are often markedly tuberculated on this account. This increase of bone formation as already shown also extends to and rounds off the orbital margin.

When a low sloping forehead and a depressed nasion are combined with massive jaws and teeth, as is often the case in the Australian aboriginal, the supraorbital ridges tend to be enormously developed (cf. Thomson (18)). Elevation of the frontal bone accompanied by a decrease of masticatory power, causes a diminution in size of this torus. The diminution first occurs over an area between the strong medial angular process and arcus superciliaris medially and the tuberculated lateral angular process laterally, to each of which, the stresses from the maxilla are directly transmitted; this intermediate area becomes the planum supraorbitale. In this region the elevated frontal bone is sufficient support without the addition of a torus.

The zygomatic arch also serves, through its inferior border, as a rod of resistance against the mandibular force as well as a support for the masseter. These factors again demand that this arch should be stout and strong.

(b) *Prognathism*. The general prognathism of the facial region of No. 792 was measured by Fraipont's method on the diagram of the norma lateralis (fig. 1). The line drawn from the glabella at right angles to the glabella-lambda line, passes in this case through the alveolus of the second incisor. Klaatsch found in the specimens of the Roth collection that it passed through the first premolar or more posteriorly; this is in agreement with Fraipont's results. No. 792 shows that the prominence of the glabella so greatly influences the position of this line that, in calvaria in which it is markedly developed, reconstruction of the facial region cannot be carried out on the assumption that the above-mentioned line will pass through the premolar region without allowing for a great margin of error (12-13 mm. in No. 792).

A second line parallel to the vertical line through the glabella and touching the most prominent point of the incisors (approximately determined owing to the teeth being absent), cuts the glabella-lambda line 4 mm. in front of the glabella (see fig. 2). This is considerably below the lowest figure quoted by Klaatsch, viz., 8 mm. in the Kalkadun skull (R. 62). Again, the prognathic angle between lines from prosthion to glabella and prosthion to inion, is  $82^{\circ}$ . The greater the facial projection the lower is this angle. Klaatsch records it as low as  $70^{\circ}$  and as high as  $81^{\circ}$  in the Roth series. Therefore, when measured



by these methods, No. 792 appears to be more orthognathic than any in the Roth series. Flower's gnathic index which is independent of the degree of development of the glabella, places it well within the limit of orthognathic skulls, the index being 95.23. Turner (19) records five orthognathous male specimens and Duckworth (7) found the range in the Cambridge Collection to be 93.4 to 108.7 in males and 95 to 108.7 in females.

Though apparently No. 792 is orthognathic, there is a decided tendency to alveolar prognathism. A measure of this was obtained by recording the angle between the following lines: (1) The line of the alveolar margin in the norma lateralis, and (2) The line from the naso-spinale to the prosthion. The angle proved to be 68°. The greater the projection of the alveolar process the smaller will this angle become.

For purposes of comparison, we have measured this angle in Klaatsch's selected specimens from the Roth series and the following results were obtained shown side by side with the figures obtained by Fraipont's method and by measuring the glabella-prosthion-inion angle:

					Distance on glabella-lambda line (Fraipont)	Glabella-prosthion in-ion-angle	Angle of alveolar prognathism of maxilla
R. 2	...	...	...	...	25 mm.	70°	64°
R. 12	...	...	...	...	11	80	62
R. 16	...	...	...	...	22	70	62
R. 24	...	...	...	...	20	72	55
R. 28	...	...	...	...	19	72	67
R. 57	...	...	...	...	24	70	56
R. 60	...	...	...	...	19	74	50
R. 62	...	...	...	...	8	81	68
R. 80	...	...	...	...	12	71	60
Stuttgart 1719	...	...	...	...	24	69	64
B. 10283 (W.A., Sydney Museum)					23	70	44
London Collection, S. 1406	...				23	73	45
No. 792	...	...	...	...	4	82	65
European (Australian Museum)					8	76	73

This table at once shows that No. 792, though orthognathic, has definite alveolar prognathism. It also shows the three types of prognathism which are possible. There may be combined (1) an alveolar projection with a general facial prognathism (R. 2, R. 24, R. 57, R. 60, B. 10283, N. 1406, R. Coll. of Surgeons), (2) an alveolar projection without a general prognathism as in No. 792, R. 80, R. 12, (3) absence of facial prognathism and also of any marked degree of alveolar projection (R. 62, European).

R. 80 and R. 12 also show that the ape-like horizontal condition of the sub-nasal region found in aboriginals is not necessarily associated with general facial prognathism, so that orthognathic skulls may thus preserve this primitive sub-nasal projection (cf. Topinard (19, 23)).

A sagittal section of the skull illustrates further the modern characteristics observed in the facial region of No. 792. The pituitary angle measured 121°

(fig. 2), so differing from the widely open angle in anthropoids, but the sphenomaxillary angle ( $90^\circ$ ) emphasises the alveolar prognathism, since this measurement is within the range of variation for the Australian aboriginal (Duckworth).

An examination of the sectional surface and interior of the cranium, reveals a number of features of interest. In the region of the bregma, the frontal bone attains a thickness of 12 mm. while both the parietal bone and the occipital in the region of the lambda are 11 mm. thick. In the vicinity of the inion, the bone is 18 mm. in thickness. These measurements are only slightly less than those of the Piltdown fossils. The texture of the diploe is, however, of a somewhat coarser nature in No. 792.

The endinion or mid-point of the cruciate eminence corresponds to a point on the planum nuchale which is 46 mm. from the opisthion. The inion is 66 mm. from the opisthion, a difference of 20 mm. (fig. 2). This low position of the posterior end of the transverse sinus closely approximates to the Neanderthal condition. Klaatsch found that the transverse sinus in the South Australian specimen (No. 1419, Stuttgart Museum) was 15 mm. below the superior curved line.

The inferior petrosal sinus on both sides forms a broad, deep channel roofed over by the petrous part of the temporal for 15 mm. on the right side and 12 mm. on the left side as it approaches the jugular foramen. The pituitary fossa is somewhat damaged, but is of normal proportions.

(c) *Palate and Mandible.* All the teeth have been lost post-mortem in No. 792. The remains of a well-marked processus molaris quarti are to be seen on each side. This process is exceeded in size by that in A. 11964 (Australian Museum), in which it is so large that it overlaps the palate bone posteriorly as a backwardly directed conical projection. The pyramidal process is comparatively well marked in our specimen, extending backwards 11 mm. from the level of the greater palatine foramen. There is a well-defined crest (torus palatinus medianus) in the mid-line of the posterior portion of the palate in several specimens, e.g., B. 10510 and A. 11964 both from the Australian Museum, Sydney, and in a young female from Queensland (*aet.* 24) (private collection). In No. 1308 (Medical School Museum) this torus expands anteriorly into a shield-like elevation of the maxilla which is limited laterally by a broad furrow, similar to the condition found in the Western Australian specimen (B. 10283) mentioned by Klaatsch, from the Australian Museum, Sydney (fig. 3 a). This torus maxillaris medianus may attain a width of 1 cm. after which it narrows towards the foramen incisivum. No. 1188, from the Medical School Museum, has a median furrow grooving the torus as in the South Australian described by Klaatsch. Extending transversely laterally from the torus maxillaris medianus at the boundary between the palatal and maxillary portions of the palate, there is in the last-named specimen a ridge (torus palatinus transversus) which reaches the medial boundary of the groove lodging the anterior palatine nerve and greater palatine artery. In No. 477,

also from the Medical School Museum, the torus transversus is continued laterally as a thin bar of bone which bridges over the groove (fig. 3*b*). From an examination of the Roth specimens, Klaatsch (12) is inclined to associate these spines and tubercles with the borders of the groove upon the palate. He states definitely that his experience failed to confirm Krause's statement that the occurrence of a trace of the torus palatinus transversus was frequent (p. 88). In the above-mentioned specimens examined by us, the transverse ridge is certainly independent of the palatine sulcus, though extending laterally to it, the site at which the junction occurs being marked by spinous processes at the borders of the groove. In Nos. 796 and 667 the arrangement of the tori of the palate is different from that above described. In these two specimens the median palatine torus, raised into a crest posteriorly, expands forwards into a V-shaped elevation, but instead of this elevation proceeding forwards as a median maxillary torus, the borders widen out at the boundary between

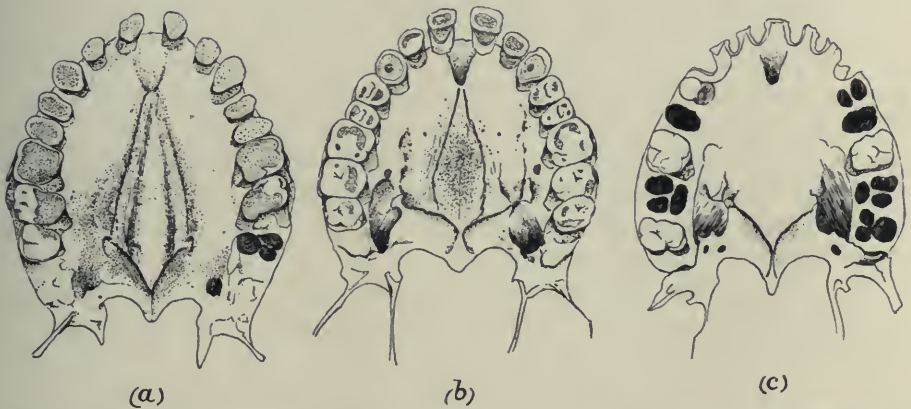


Fig. 3. Showing of arrangement of the tori palatini and maxillaris of the palate of Australian skulls. (a) No. 1308; (b) No. 477 (Medical School Museum); (c) No. 796.

the palatal and maxillary portions of the palate to become continuous with the transverse palatine torus. The maxillary torus is thus indistinguishable as a distinct elevation upon the palatal processes of the maxilla (fig. 3*c*). When well developed, these tori probably serve as additional supports for the force transmitted to the palate through the lingual roots of the molar teeth (fig. 9). In Nos. 620, 607 and 792 the tori are not well marked. There is a faint median crest representing the torus palatinus medianus posteriorly which diverges when traced forwards into a series of tubercles. These may be looked upon as constituting the torus palatinus transversus, which forms the posterior boundary of the flattened torus maxillaris medianus in the above-mentioned specimens. In No. 792 as in many Australian skulls a curved sharply defined crest for the tensor veli palatini (crista palatina transversa) is to be seen behind the transverse torus of the palate.

The shape of the palate indicates that this structure is of the modern type.



The palato-maxillary index of Flower is 120.6, so placing it in the brachyuranic group. The palatal width is 70 mm. and the palato-maxillary length is 58 mm.; these measurements are almost identical with those of the remarkable Mudgee skull described by Turner (71 and 58 mm. respectively) in which the index was as high as 122.

The mandible in No. 792 presents several features of interest in the region of the angle. The lower border curves gently backwards and inwards. The outer edge of this border is everted over an extent of 30 mm., the maximum projection being on the left side where it is 3 mm. (apophysis lemurica). On the inner surface of the angle there is a series of ridges (five on the right and eight on the left) here and there raised into as many spinous projections. These external and internal projections meet along the posterior border in a distinct tubercle. The same features are seen to an equal degree in No. 477; the apophysis lemurica is, however, developed to a much greater degree in the mandible belonging to No. 667 from the Hawkesbury District (N.S.W.).

Convex downwards the inferior border of the body continues backwards into the angle of the ramus which is gently rounded. A similar gentle curvature is present at the continuation of the alveolar margin into the anterior border of the ramus, but the general direction of the anterior border of the latter is approximately at right angles to the body. The medial aspect of the ramus shows anthropoid characteristics. An exceptionally well-marked ridge extends from below the tip of the coronoid process to the alveolar border. Behind this only the slightest indication of a fossa sub-coronoidea is present, but in front between this ridge and the anterior border of the ramus a deep groove is seen, the lower part of which groove is visible from the lateral aspect between the anterior border of the ramus and the socket for the third molar. This interval behind the 3rd molar (diastema molaris quarti) is 7 mm. as compared with 9 mm. in R. 2, the latter being one of Klaatsch's most marked cases. There is also a triangular backward extension of the alveolar margin (*circa* 6 mm.) claimed by Zuckerkandl (26) and Prof. J. T. Wilson (25) as indicating the previous existence of a fourth molar. Klaatsch regards the diastema as being a more important indication. It is to be noted that the two features are often present in the same skull (R. 2, R. 12, R. 57, R. 60 and the W.A. No. B. 10283, Sydney Museum). It is also to be noticed that the skulls with the most marked processus molaris quarti often have a correspondingly well-marked interval and triangular alveolar extension in the lower jaw (R. 2, R. 12, R. 44, R. 88 and No. 792).

R. 57 exemplifies the primitive parallel arrangement of the molar teeth on each side of the lower jaw, for as Klaatsch noted the distance between the first premolars was in this case 33 mm. and between the third molars was 40 mm. a difference of only 7 mm. In No. 792 the difference is 26 mm., the measurements being 24 mm. by 50 mm. respectively. These features and others, viz., the size of the ramus and the proportions of the coronoid and condyloid processus indicate that the mandible of No. 792 is distinctly modern.



The chin is moderately well marked (fig. 1) and the genioïd spines present a considerable degree of prominence. The alveolar chin angle (Klaatsch) between the line of the alveolar border and the tangent from the mental protuberance to the anterior point between the incisors is  $88^{\circ}$ . This angle in our opinion does not give a conception of the degree of prognathism of the alveolar process of the mandible, for on inspection from behind, this process is seen to slope definitely forwards and upwards, corresponding with the alveolar prognathism of the maxilla already described. Except in a case such as No. 2165 (Medical School Museum) in which the chin is ill-defined and non-projecting, the development of the mental process obscures this forward slope when the mandible is viewed from the front and makes the alveolar chin angle approximate to  $90^{\circ}$ . We have therefore measured the angle included between the alveolar line and the line from the anterior point between the incisors to the lowest median point on the lower border of the body of the mandible in the mid-line (gnathion). The resulting angle in No. 792 is  $76^{\circ}$ , an angle which indicates more accurately than the "alveolar angle" the degree of alveolar prognathism.

In R. 2, in which the two lines used by Klaatsch are at right angles, we find the alveolo-symphysial angle to be  $81^{\circ}$ . This indicates the degree of forward slope of the alveolar process which is apparent on inspection. Examination of other Roth specimens confirmed this result. A consideration of the alveolo-symphysial angle together with the angle of alveolar prognathism of the maxilla, gives a true indication of the degree of "snoutiness" of the Australian aboriginal skull. It is specially worthy of note that the muzzle-like condition of the face may be present in an orthognathic skull such as No. 792 (cf. Topinard (19)).

## II. THE CRANIAL SKELETON

(a) *The Temporal and Sphenoidal Region.* The mastoid process is better developed in No. 792 than is usually the case in the aboriginal skull. The left process is somewhat more projecting but at a higher level than the right, the latter feature is part of a general asymmetry. The mastoid crest is continuous with the linea nuchae superior; though the latter is extremely well marked, the bridge uniting the mastoid process with it is not nearly so pronounced as in R. 60, especially referred to by Klaatsch. On this account the supra-mastoid crest is only moderately developed and an interval of 22 mm. separates it from the mastoid crest, again being unlike R. 60, in which the distance is only 10 mm.

In the region of the lambdoid suture is a rounded but well defined ridge, extending upwards and backwards for a distance of 21 mm. (fig. 6). Superiorly this ridge can clearly be traced into continuity with the superior temporal line, while inferiorly it blends with the crista mastoidea and passes towards the anterior border of the mastoid process. This then must be regarded as the actual termination of the superior temporal line in No. 792. Diverging from

this line in the region of the lambdoid suture as it is traced upwards, is a well-marked *linea nuchae suprema*. Thus the crista muscularis of the adult male gorilla is represented in No. 792 by four distinct lines—the temporal portion by the superior and inferior temporal lines and the occipital portion by the supreme and superior nuchal lines. The affinity with the anthropoid condition is shown by the close approximation of the posterior three lines for a distance of 50 mm. in the mastoid region (see fig. 7). Moreover in R. 60 and R. 24 there is a close approximation of the supra-mastoid crest to these three lines. In B. 3714 (Australian Museum), actual fusion of the four lines has occurred for a distance of 28 mm. producing a rough elevated area in the region of the asterion 14 mm. in width. This closely simulates the condition in the young anthropoid. Aboriginal specimens are thus met with in which the superior temporal line after continuing inferiorly, skirts the lambdoid suture in order to cut the parieto-mastoid suture about 10 mm. in front of the asterion. This may then become, as pointed out by Wilson (24), continuous with the mastoid crest (No. 792, No. 477, Medical School Museum; R. 2, R. 16, R. 24, R. 36, R. 60, No. 1245 and B. 3714, Australian Museum). In the majority of the above skulls including No. 792, the posterior inferior angle of the parietal bone is distinctly ridged by this continuation, recalling the considerable degree of prominence of the crista muscularis in the region of the asterion in anthropoids.

The parieto-sphenoid articulation is present and measures 5 mm. on the right side and 8 mm. on the left. The parieto-temporal suture has a more horizontal course than in the modern European, but the junction between the squamous and mastoid portions is clearly indicated (fig. 7). It is to be noted that the fronto-sphenoid articulation lies on a level with the zygomatico-frontal suture, i.e. at a somewhat lower level than is usually the case in modern skulls. The level of this suture is even still lower in the Anthropoids.

Klaatsch's method of measuring the post-orbital depression on the glabella-inion horizon was followed and the annexed table incorporates his figures for purposes of comparison:

	R. 24	No. 792	Pithecan- thropus	Spy I	Spy II
Post-orbital depression ...	90	91	87	104	103 mm.
Supra-orbital breadth ...	120	112	106	123	124 mm.
Index of the post-orbital depression $a \times 100/b$ ...	75	81.25	82.08	84.55	83.06
Distance of the post-orbital depression from the gla- bella ... ..	50	44	35	37	39 mm.

The above measurements illustrate the similarity of the Australian skull with the Spy, Neanderthal and Pithecanthropus specimens in the sphenoidal regions. None of the measurements, however, are outside the range of those found in the aboriginal skulls of the Roth collection. For instance, the distance of the post-orbital depression from the glabella, exceeds that found in the Spy specimens and also Pithecanthropus, all of which have a measurement

between 35 and 40 mm. Several skulls of the Roth collection were found by Klaatsch in which the distance was between 45 and 50 mm. (R. 24, R. 28, R. 57, R. 62). All these examples contrast with the European where the depression is usually placed closer to the glabella (Schwalbe, quoted by Klaatsch). Klaatsch measured the greatest supraorbital breadth, i.e., the distance between the ectorbital prominences which overhang the fronto-zygomatic suture. The degree of development of the external angular process is then given by comparing this measurement with the post-orbital diameter. The smaller the index the larger and more prominent is the external angular process and we may note that the index in No. 792 is slightly below that of *Pithecanthropus* and the Spy skulls.

(b) *The Cranial Vault*. In No. 792 the distance of the inferior temporal lines from the sagittal suture in a projection is 45 mm. in the frontal region (fig. 1); in the anterior parietal region it is approximately the same (45.5 mm.). The two temporal lines are separated from one another by a distance of 5 mm. even when only a short distance above the fronto-zygomatic suture. They diverge somewhat from one another and at the coronal suture are separated by an interval of 15 mm. On crossing this they both deviate upwards and skirt the upper margin of the parietal eminence.

The interval between the temporal lines is occupied by a well-marked bregmatic eminence forming a diamond-shaped area somewhat spread out both from side to side and from before backwards, approximating to the condition found in the W.A. B. 10283 (Australian Museum) skull. The anterior angle of this eminence which can be traced forwards to the supra-orbital depression forms a torus frontalis medianus.

Posteriorly the bregmatic eminence continues to the vertex (fig. 7); the highest point of the eminence is situated behind the bregma. The general form of the eminence in No. 792 is intermediate between the broad, flat elevation seen in the female Tasmanian in the Australian Museum and the more sharply defined eminence of *Pithecanthropus*. E. 11348 and S. 1158 (Australian Museum) have a similar eminence to No. 792, but it is separated posteriorly by a distinct depression from the vertex as in *Pithecanthropus* and R. 60. The receding forehead presents on either side of the torus frontalis medianus practically no signs of tubera frontalis.

In No. 792 the parietal eminences although present, are ill-developed, the interparietal diameter (117 mm.) being 15 mm. less than the greatest width (132 mm.) which coincides with the supramastoid breadth.

Turner (21), referring to the parietal bone in the Tasmanian aboriginal, states that "in the postero-parietal region a broad, shallow, median depressed area exists, bounded laterally by a low ridge on the parietal bone and along the middle of this depression the sagittal suture lies below the general plane of the vault." This condition is also to be observed in the skull of the Australian aboriginal, e.g., in No. 791, No. 618, R. 78, R. 45, R. 17, R. 14, R. 8 and R. 12, but is absent in No. 792.



The forward projection of the lateral part of the lambdoid suture found in the Neanderthal skull and some anthropoids, is remarkably well seen in No. 792 (fig. 8). This projection reaches to the same level as the lambda. In R. 7 and S. 1157 (Australian Museum) this projection is well shown on the right side while corresponding to it on the left side there is an intercalated bone. This association with intercalated bones is not uncommon as was pointed out by Klaatsch. There is a transverse occipital suture on both sides in No. 792 extending medially from the lambdoid suture for 15 mm.

An examination of the occipital region of No. 792 reveals a well-marked torus occipitalis transversus. Like several Roth specimens, e.g., (R. 60, R. 62, R. 80) the lower border of this torus in No. 792 is situated at a higher level than the sulcus transversus. The external occipital protuberance is not developed; the torus is continuous as an uniform elevation across the mid-line. In No. 477 (Medical School Museum) there is a torus of an even greater degree of development which presents two lateral tubercles. In the mid-line it also projects downwards into a V-shaped external occipital protuberance. The upper border of the torus in No. 792 representing the linea nuchae suprema is separated by a shallow groove from the remainder of the squama occipitalis. Two centimetres from the mid-line the torus presents on each side a prominent tubercle which is more projecting than the median portion of the torus. The internal aspect of the occipital at this point shows the impression of the occipital lobe of the brain, more marked on the left side, where the thickness of the bone is 10 mm.; this is to be compared with the maximum thickness in the mid-line which was found to be 18 mm. The lower border of the torus (linea nuchae superior) forms a thick rounded edge; a shallow groove separates it from the upper portion while it forms inferiorly a rolled projecting border, over which the planum nuchale passes into the squama occipitalis. The muscular impressions upon the planum nuchale reach only a moderate degree of development in this specimen.

The cubic capacity of No. 792 measured by chilled shot in the usual manner, was 1218 c.c. The water displacement of a cast made later after the skull had been sectioned was 1211 c.c. Turner (20) found that the mean eubic capacity of 34 adult crania in his series was 1230 c.c. Duckworth determined the average cranial capacity of the adult Australian aboriginal to be 1246.5 c.c. from measurements on 150 skulls.

The skull is markedly dolicho-cephalic, the cephalic index being 65.02. It is also markedly phenozygous as already indicated (fig. 9).

#### *The General Relative Proportions of the Cranium*

Horizontal curves on the glabella-inion plane, on a plane 20 mm. above this and at the point of deepest depression of the nose, were made with the aid of Lissauer's diagraph, the maximum projection of the superciliary ridges being also shown (fig. 2).

The usual flattening of the temporal and sphenoidal regions found in

Australian aboriginals is not so marked in No. 792, which approaches the condition met with in the exceptions in the Roth collection mentioned by Klaatsch (R. 2, R. 16 and W.A. B. 10283) which he points out is a permanent feature. It is to be noted that the asterionic diameter exceeds the stephanic by 11 mm. Transverse curves were drawn in a like fashion through the bregma and the vertex with the skull oriented in the glabella-inion plane (fig. 5). Both the height of the bregma (91 mm.) and the vertex (98 mm.) are well within the range found in Australian aboriginals.

The maximum occipital point coincides with the inion. A massive torus combined with an elevation of the inion gives a pithecoïd appearance to the occipital region. Coincidence of the inion and maximum occipital point which



Fig. 4. Horizontal sections of Australian skull (No. 792). (a) At the level of the glabella-inion plane (interrupted line). (b) On a plane 20 mm. above the glabella-inion plane (dotted line). The greatest forward projection of the superciliary ridges is also indicated and the most depressed point of the nasal region. Also the position of the various sutures as they occurred.

is seen in *Pithecanthropus* and the Neanderthal is also exhibited in R. 2 and R. 60 (Klaatsch), R. 9, S. 1158, E. 11348, No. 791, No. 796 and a Tasmanian calvarium, No. 1254 (Australian Museum). In consequence of this, the maximum cranial length in these skulls is identical with the glabella-iniac length. In the specimens mentioned this length ranges between 182 mm. (R. 2) and 192 mm. (F. 11348), the Tasmanian specimen measuring 184 mm. and *Pithecanthropus* 181 mm. No. 792 on the other hand has a length of 203 mm. The longest Australian male cranium described by Turner measured 200 mm. (Challenger series 20). This length was considered by Turner to be remarkable. He quotes, however, cases which had an even greater length, e.g., Miklucho-Maclay's specimen which measured 204 mm. in length and that of Davis 210 mm. The sutures in skull No. 792 though simple, are normally developed.

There is no sign of closure of the sagittal suture as in Miklucho-Maclay's specimen. The maximum occipital length in No. 792 exceeds in length the Neanderthal (200 mm.), Spy I (200 mm.), and Spy II (198 mm.). It will, therefore, be seen that the calvarium of No. 792 resembles the Neanderthal fragment, both in its absolute length and in the fact that the maximum occipital point coincides with the inion. The general appearance of the cranium, however, differs from the Neanderthal fragment, in that platycephaly is apparently not a marked feature in No. 792 and the marked lateral bulging posteriorly is not reproduced. On measurement, the cephalic and vertical indices are found to be approximately equal, 65.02 and 65.07 respectively.

It is interesting to note that there is combined with this dolicho-platycephaly, marked projection of the superciliary ridges and glabella. In regard to this Turner (19, p. 49) says, "the strongly projecting supraciliary ridges and glabella which have been described as characteristic features in the dolicho-platycephalic crania, are by no means confined to them."

It may be noted that Huxley's Western Port skull also had a cephalic index of 73 and a vertical index of 73.6 (8, 9). Quatrefages and Hamy (15) classify the skull presented by M. Erklund to the Museum Retzius as dolicho-platycephalic. The cephalic and vertical indices are 64.6 and 64.1 respectively. He contrasts these measurements with those of a skull of the ordinary Australian type, in which the length-breadth index is 67.0 and the vertical index 73.19. In this connection a *resumé* may be given of the characteristics of a skull from Port Fairy, Victoria, in the Australian Museum (No. 1245) and described by Quatrefages and Hamy. The glabella-inion length is 194 mm. while the maximum length is 206 mm. due to a backward bulging of the squama occipitalis. The maximum breadth, which is the supra-mastoid diameter, is 142 mm. compared with a basi-bregmatic height of 131 mm., giving a cephalic index of 68.44 and a vertical index of 63. These indices indicate a condition of marked dolicho-platycephaly. A fossa pre-lambdaidea is present in the Port Fairy skull as would be expected on account of the marked backward bulging of the squama occipitalis, the glabella-lambda length (200 mm.) being greater than the glabella-inion length (194 mm.). This fossa is also well represented, however, in No. 792, although the squama is directed not backwards but slightly forwards, the glabella-lambda length (194 mm.) being less than the glabella-inion length (203 mm.).

An idea of the direction of the squama is obtained by measuring the angle between the glabella-inion and inion-lambda, which is  $72^\circ$  compared with  $67^\circ$  in the Neanderthal and Spy I skulls,  $70^\circ$  in Spy II and  $71^\circ$  in R. 2, the lowest of the Roth series. The smallness of this angle is another indication of the primitive formation in the occipital region. The opisthionie angle is  $33^\circ$ . The planum nuchale slopes upwards and backwards to the inion (in the median plane). It has an absolute length greater than that of the squama occipitalis, the measurements being respectively 66 mm. and 56 mm. These two features further emphasise the pithecoïd appearance.



The curvature of the occipital measured by the distance of the lambda-inion line from the most prominent point of the curvature of the planum occipitale is shown in No. 792 to be intermediate between *Pithecanthropus* and the Neanderthal specimen (Table VII). The preservation of this small degree of curvature is not uncommon in aboriginal skulls as shown by the Roth collection.

The angle between the glabella-inion and the glabella-lambda lines is below the range for the Australian and other races ( $17^{\circ}$ – $22^{\circ}$ ; Klaatsch). It is the same as that of the Neanderthal fragment, viz.  $15^{\circ}$ . This angle points to the comparative shortness of the planum occipitale which subtends this angle.

In addition to the primitive formation in the occipital region, there is, as has already been pointed out, a remarkable recession of the forehead. The following measurements of the bregma-glabella-inion angle (Schwalbe) are significant: No. 792,  $50^{\circ}$ ; R. 2,  $56^{\circ}$ ; South Australian,  $51^{\circ}$ ; West Australian,  $56^{\circ}$ ; *Pithecanthropus*,  $41^{\circ}$ ; Neanderthal,  $45^{\circ}$ ; Spy I,  $46^{\circ}$ ; Spy II,  $47^{\circ}$ ; Klaatsch stated that the range for Australian aboriginals was  $51^{\circ}$  to  $62^{\circ}$ . However, fig. 8 a of Berry and Robertson's tracings of Australian crania<sup>(3)</sup> exhibits an angle of  $49^{\circ}$ . From the above figures it will be seen at once that the forehead region in No. 792 approaches more closely to that found in the Neanderthal race than in R. 2, the S.A. (Stuttgart) and the West Australian (the lowest recorded by Klaatsch). In order to indicate more fully the slope of the forehead, the index of curvature of the frontal is recorded in these cases, i.e., the comparison between the glabella-bregma length and the distance of this line from the most prominent point of the frontal. Like R. 2 and the W.A. No. 792 falls within the range of variation of the Neanderthal specimens. On the other hand the South Australian specimen has a considerable degree of curvature of the frontal despite its low bregma-glabella-inion angle, a fact which illustrates the necessity of measuring the index of curvature of the frontal. The degree of frontal slope may be measured also by estimating Schwalbe's forehead angle, which is included between the glabella-inion line and the tangent from the glabella to the most prominent part of the surface outline of the frontal. This angle is  $98^{\circ}$  in the S.A., as compared with  $67^{\circ}$  in Spy II. In No. 792 it is only  $70^{\circ}$ , which indicates a stage of forehead slope between the lower limit for modern races and the Neanderthal race. The W.A. skull has the lowest measurement of any Australian skull of the Australian Museum series, viz.,  $74^{\circ}$ . The very low angle in No. 792 is due to the fact that the point of maximum curvature of the frontal is situated more posteriorly than in some specimens which have a lower index of curvature.

In R. 2 the degree of frontal curvature is less than in No. 792, for the maximum elevation of the frontal above the glabella-bregma chord is only 13 mm. in the former compared with 15 mm. in the latter; the index obtained by comparing this with the length of the chord being 12.5 and 13.04 respectively. The forehead angle in R. 2 is, however,  $79^{\circ}$ , due to the fact that the

maximum point of curvature is situated more anteriorly than in No. 792. The more posteriorly this point is placed, the more primitive is the appearance of the sloping forehead. Comparable to No. 792 in this respect is the West Australian skull, which has been seen to have a forehead angle of  $74^\circ$ , the index being 13.2.

The bregma-nasion-inion angle was measured in No. 792 to compare the degree of slope of the forehead with that of the New South Wales specimen (xxix. B. 12, Turner series) described by Cunningham (5). It was found to be  $54^\circ$ , as compared with  $53^\circ$  in the New South Wales specimen. Applying the method used by Cunningham for obtaining the frontal index of curvature, viz., comparison of maximum height of the frontal above the line joining the nasion and bregma, with the distance between these two points, we found that this index in No. 792 was 20. In the New South Wales specimen this index is 15. These two measurements indicate a more receding forehead in the skull described by Cunningham than in No. 792.

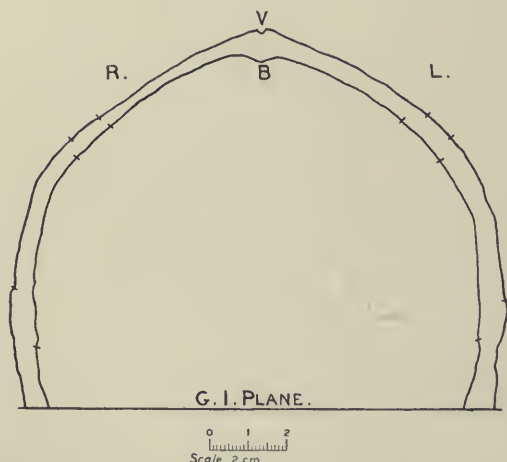


Fig. 5. Vertical sections of Australian skull (No. 792) from the glabella-inion plane to the bregma (B) and the vertex (V). The temporal lines and squamosal suture are indicated.

In No. 792 the height of the bregma above the glabella-inion line is 90 mm. giving an index when compared with the glabella-inion length of 44.23. The lowest index in the Roth series was 47.25 (R. 2). Klaatsch (12, p. 139), however, found that the South Australian specimen had an index of 44.79. This latter skull and also one from North Queensland, he found "nearest to the type of fossil European man" of the skulls he examined.

The height of the vertex of No. 792 is 98 mm. giving an index when compared with the glabella-inion length of 48.27, which is less than that of the South Australian skull. It is to be noted that both the index of the height of the bregma and of the vertex of No. 792 reach their low limit on account of the great glabella-inion length.

## SUMMARY AND CONCLUSIONS

The outstanding features of the skull No. 792 are:

- (i) The general massiveness of the skull including the great thickness of the cranial vault.
- (ii) The receding forehead.
- (iii) The great absolute length of the cranium.
- (iv) The massive undivided tori supraorbitales, and the marked projection of the glabella in the region of which unusually large frontal air-sinuses separate the two tables of bone.
- (v) The pitheccoid conformation of the occipital region and the presence of a well-defined torus occipitalis.

The face is less primitive than the cranial vault exhibiting orthognathism and a leptorrhine nasal region.

Special reference has been made to the Neanderthaloid features of the specimen. The resemblances of the cranium to the Neanderthal specimen is remarkable when the marked contrast of the general skeleton of the two types is kept in mind. We must regard the cranial resemblances as an expression of the principle that descendants of a common ancestor show a tendency to develop independently similar features.

The Neanderthaloid features of No. 792 are as follows:

- (1) The degree and projection of the glabella and tori supraorbitales, the latter being undivided (Type III, Cunningham).

The index of post-orbital depression is 81.25 (Pithecanthropus, 82.08; Spy II, 83.06) and the distance of the post-orbital depression from the glabella is 44 mm. (Pithecanthropus, 35; Spy II, 39).

- (2) The presence of the fossa supraglabellaris and sulci supraorbitales.
- (3) The degree of forehead slope. (Bregma-glabella-inion angle 50° (Spy II, 47°); Schwalbe forehead angle 70° (Spy II, 67°). Index of curve of frontal 13.04 (Neanderthal, 13.39; Spy I, 10.10; Spy II, 15.92).)
- (4) The great length of the precerebral part of the roof of the orbit. (No. 792, 25 mm.; Neanderthal, 20 mm.)
- (5) The presence of a bregmatic eminence.
- (6) The presence of the torus occipitalis transversus with tubercles situated laterally.
- (7) The low position of the endinion (20 mm. below inion).
- (8) The contour of the lambdoid and temporal sutures.
- (9) The rounded outline of the temporal and sphenoidal regions, as depicted in horizontal and vertical sections.
- (10) The coincidence of the inion and maximum occipital point, combined with the great absolute length of the glabella-inion line (203 mm.).
- (11) The fact that the skull is dolicho-platycephalic as shown by the low cephalic index (65.02) and the equality of the cephalic and vertical



indices, although the flattened appearance of the Neanderthal is absent.

- (12) The forward slope of the planum occipitale as measured by the glabella-inion-lambda angle, viz. No. 792, 72°; Spy II, 70°; Neanderthal and Spy I, 67°.
- (13) The low indices both of the height of the bregma (44·23) and of the vertex (48·27).
- (14) The angle between the glabella-inion and the glabella-lambda (15°) is the same as in the Neanderthal.

Of the above features, the development of the tori supraorbitales and glabella, the fossa supraglabellaris and sulci supraorbitales, and the well-defined diamond-shaped bregmatic eminence, show a resemblance to *Pithecanthropus*.

It is thus seen that it is the calvarium of No. 792 which retains primitive features. The facial skeleton presents paradoxically modern features. Therefore this specimen illustrates, as Turner (20, p. 49) indicated, that specialisation in some directions may be accompanied by a marked lack of specialisation in other respects in one and the same skull.

The general survey of Australian skulls, undertaken for purposes of comparison with No. 792, led to conclusions which may be summarised as follows. The diamond-shaped appearance of the face, commonly found in the Australian, owing to the prominence of the zygomatic bones and curvature of the zygomatic arch, is developed as a result of the increase in these bones to provide a base of resistance during mastication, and to support the masticatory muscles. Further the explanation of the rolled character of the inferolateral margin of the orbit was attempted by correlating this condition with the size and degree of wearing of the teeth. Finally the considerable variability in the degree of development of the infraorbital fossa is found to be due to the varying conditions connected with the direction of the masticatory thrust from the different groups of teeth.

The principal measurements of No. 792 are:

Cubic capacity, 1211 c.c.; maximum length (glabella-inion), 203 mm.; maximum breadth, 132 mm.; cephalic index, 65·02; basi-bregmatic height, 133 mm.; vertical index, 65·07; auriculo-bregmatic height, 111 mm.; glabella-lambda line, 194 mm.; nasion-inion line, 195 mm.; basion-nasion line, 107 mm.; prosthion-basion line, 99 mm.; minimum frontal breadth, 90 mm.; maximum frontal breadth, 103 mm.; asterionic diameter, 111 mm.; interparietal diameter, 117 mm.; stephanic diameter, 100 mm.; supranastoid breadth, 132 mm.; nasal height, 55 mm.; nasal width, 26 mm.; nasal index, 47·2; height of apertura piriformis, 35 mm.; index of apertura piriformis, 74·3; height of choanae, 39 mm.; width of choana, 19·5 mm.; orbital height, 35 mm.; orbital width, 39 mm.; orbital index, 89·75; minimum interorbital distance, 18 mm.; inter-zygomatic breadth, 139 mm.; palatal length, 52 mm.; maxillary breadth, 94 mm.; length of os palatinum, 17 mm.; depth of palate at M. 1,

13 mm.; basi-alveolar length, 100 mm.; basi-nasal length, 105 mm.; gnathic index, 95.23; symphyseal height, 27 mm.; angle of the ascending ramus, 113°; coronoid height, 73.5 mm.; minimum breadth of the ramus, 32 mm.; bigonial width, 104 mm.; inter-coronoid width, 104 mm.; inter-condyloid width, 119 mm.

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## EXPLANATION OF FIGURES

*As.* Asterion; *B.* Basion; *Br.* Bregma; *End.* Endinion; *Gn.* Gnathion (Wilder); *Gl.* Glabella; *I.* Inion; *L.* Lambda; *M.F.* Mental Foramen; *N.* Nasion; *Ns.* Nasospinale; *O.* Opisthion; *Po.* Porion; *Pr.* Prosthion; *Ps.* Prosphenion; *Sph.* Sphenoidale; *V.* Vertex.

Figs. 6-9. Various normae of Australian skull (No. 792).

## SKULLS REFERRED TO IN THE TEXT

I. *Anatomy Department Collection*

No. 792. Tamworth, N.S.W. No. 607. Little Manby, Sydney, N.S.W. No. 618. Little Manby, Sydney, N.S.W. No. 620. Botany, Sydney, N.S.W. No. 667 (Hawkesbury District, N.S.W.). No. 791 (Dashino Downs) Queensland. No. 793. Central Australia (?). No. 795. N.S.W. No. 796. N.S.W. (?).

II *Medical School Museum*

No. 477. Kyogle, N.S.W. No. 1188. Northern Australia. No. 1308. Port Jackson, Sydney, N.S.W. No. 2165. No data. No. 2355. Port Hacking, N.S.W. No. 2356. Port Hacking, N.S.W.

III. *Australian Museum, Sydney*

B. 10283. ♂, Western Australia with fourth molars in upper jaw. No. 1245. Port Fairy, Victoria. E. 11348. Lake Victor, N.S.W. S. 1157. Jervis Bay, N.S.W. S. 1158. Gurdogai, N.S.W. B. 3714. No data. S. 404. Tasmanian No. 1254. Tasmanian B. 10510. Cairns, Queensland. A. 11964. Queensland.

A. 11964; R. 2, ♂; R. 5, ♂, R. 7, ♂; R. 8, ♀; R. 9, ♂; R. 10, ♂; R. 12, ♀; R. 14, ♂; R. 15, ♂; R. 16, ♂; R. 17, ♂; R. 24, ♂; R. 25, ♂; R. 28, ♂; R. 35, ♂; R. 36, ♂; R. 38, ♂; R. 39, ♂; R. 44, ♀; R. 45, ♂; R. 49, ♀; R. 57, ♂; R. 58, ♂; R. 60, ♂; R. 62, ♂; R. 69, ♂; R. 78, ♂; R. 80, ♂; R. 82, ♀; R. 87 (child); R. 88, ♂, Queensland.





Fig. 6



Fig. 7

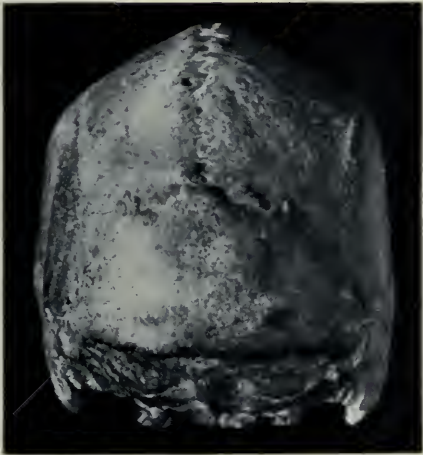


Fig. 8

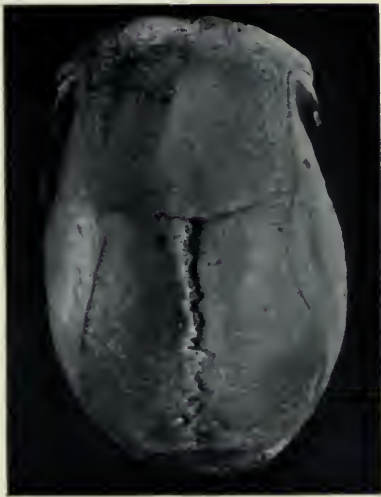


Fig. 9



# ODONTOLOGICAL ESSAYS

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## FIFTH ESSAY

### ON THE RELATION BETWEEN REPTILIAN AND MAMMALIAN DENTITION

IN the previous essay I expressed my views upon the relationship between the simple teeth of Reptiles and the composite teeth of Mammals, and the manner in which the latter were evolved from the former. Although I made some allusion to the relationship between reptilian and mammalian dentitions as a whole yet I pleaded that criticism of the views expressed in that essay be suspended until my more complete considerations on the dentitions of the two groups were published.

In the present essay I will endeavour to make good the contention that tooth-succession in the mammal is a phenomenon entirely different from that occurring in the reptile. The contention is based upon certain hitherto undiscovered facts, ascertained as a result of an exhaustive investigation on tooth development in reptiles.

In comparing reptiles and mammals the Marsupials will not be taken into account. As is well known the marsupial dentition is entirely different from that of mammals and any attempt to homologise the functional dentitions of these animals is a task of considerable difficulty. The reason for such difficulty will become apparent later, but I may be justified in eliminating its present consideration on the following grounds. An investigation on the development of the teeth in marsupials has convinced me that these more primitive mammals occupy, as regards their dentition, a position intermediate between the Reptilia and the Eutheria; in other words the Metatheria resemble the reptiles in some respects and the Eutheria in others. This fact appeared to me of such importance as to require a special essay upon tooth-development and tooth-succession in marsupials. This essay will be published in due course.

A short summary of current opinion concerning the relationship between tooth-succession as it occurs in reptiles and placental mammals respectively may precede the exposition of my own views.

The fundamental difference between the dentitions of the two groups is shown by the fact that in reptiles tooth-succession is unlimited, whilst in most Placentalia one succession of teeth alone eventuates and in some of them no succession occurs at all. These differences are expressed by the terms: polyphyodont, diphyodont and monophyodont. The two dentitions of diphyo-



dont mammals are distinguished as the milk dentition and the permanent dentition respectively.

In the case of monophyodontism it is not always certain to which of the two the functional dentition belongs. For instance Kükenthal considers the functional teeth of Cetaceae to be a milk dentition. In other cases, as in Talpa, tooth-succession occurs before birth, and the functional teeth belong to a second or permanent series. The investigations of Leche show that the functional dentition of Erinaceus is mixed, containing elements of both dentitions. Such cases, however, may be regarded as exceptional, as two dentitions, a milk and a permanent, occur normally in mammals. It is commonly held that the two dentitions of mammals are homologous with two tooth-generations of reptiles, that the diphyodontism of mammals proceeded from the polyphyodontism of reptiles by a diminution of the unlimited succession of teeth peculiar to these vertebrates; and that the difference between the two groups of vertebrates is of a purely quantitative nature, monophyodontism being considered as a further stage in the process of diminution. This view is supported by Marett Tims, who summarises current opinion by presenting in Tomes' *Manual*, 7th edition, p. 362, a very suggestive diagram of the interpretation of mammalian dentition.

In a recent communication Broom<sup>1</sup> lays stress upon a fact which apparently establishes the correctness of the above mentioned relationship between mammalian diphyodontism and reptilian polyphyodontism. Of all reptiles the extinct group of Cynodontia are recognised as exhibiting the nearest relationship to mammals. Broom, describing tooth-succession in a nearly adult specimen of *Diademodon platyrhinus*, demonstrates that there is close agreement between it and the normal appearances in mammals. However, I am of the opinion that this agreement is insufficient to prove the identity of the process of tooth-succession in mammals and reptiles. Broom's observations prove that in Cynodontia a succession of teeth occurs but once only. Such a phenomenon is by no means remarkable as in certain recent reptiles, Calotes may be cited as an example, tooth-succession occurs very slowly indeed. That some reptile or other exhibits but one single tooth change is not conclusive evidence that the character of this process in reptiles and mammals is identical. Nevertheless, the succession of teeth in Cynodontia seems to me a phenomenon worthy of careful consideration, since the possibility of the process of tooth change in this group of reptiles harmonising in some respects with that in marsupials must be taken into account, as the marsupials occupy a position intermediate between the Placentalia and the Reptilia.

The hypothesis of a direct relationship between reptilian and mammalian tooth-succession has already been accepted as a dogma and its truth has never been questioned. Labouring under the thralldom of this conviction many investigators have studied tooth-development in mammals with the avowed

<sup>1</sup> "On Evidence of a mammal-like dental succession in the Cynodont Reptiles." *Bull. Am. Mus. Nat. Hist.* vol. xxxii. 1913.

object of discovering vestiges of additional dentitions. A considerable literature exists in which the germs of hypothetical premilk or post-permanent dentitions are described. While agreeing with those authorities who throw doubt upon the validity of the appearances described as proving such additional dentitions, I further deny their possibility on fundamental grounds. My opinion as to the significance of epithelial excrescences and protuberances differs entirely from that of other investigators who interpret them as vestigial germs of an abortive dentition. I have already demonstrated that the epithelial formations regarded as evidence of a premilk dentition are in reality partly rudiments of the teeth glands in reptiles (*vide* Essay III) and partly fragments of the external enamel strand (*vide* Essay II). My views concerning the germs which are presumed to indicate a potential post-permanent dentition, will appear in a subsequent essay.

With this introduction the discussion of the subject matter of the present essay can now be approached.

If the first toothgerms appearing upon the dental lamina of a reptilian embryo be carefully studied one is struck by the fact that these germs do not all behave in the same manner. In order to prove this I will describe the peculiarities of the first teeth in the upper jaw of a *Crocodylus porosus*. In fig. 108, eight sections through the germ of such a tooth are represented. In

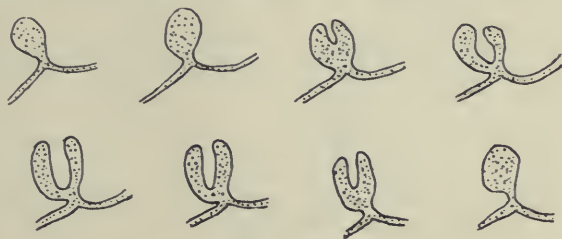


Fig. 108.

the first section the toothband, still rather short in this stage, is, as a whole, swollen and its thickening is apparently symmetrical. The dentine-papilla, seen in the further sections, also seems to be symmetrically disposed, and has apparently pushed its way in at the distal end of the thickening, the enamel-organ having assumed the well known form of a bell.

The toothgerm next in order, of which eight sections are also represented (fig. 109), shows, however, a somewhat different relationship between the dentine-papilla and the enamel-organ. The tooth-band is swollen up, as in the first germ, but in this case the thickening is evidently asymmetrical. Further it must be particularly noticed that the dentine-papilla has pushed its way into the lateral or buccal side of the enamel-organ and not at its distal end.

The different behaviour of the dentine-papilla in the two toothgerms gives one the impression that one of the toothgerms is formed from the border of the dental lamina, the other from its buccal side. As far as the latter is

concerned this is really the case, the toothgerm represented in fig. 109 being without any doubt a formation on the lateral side of the toothband.

I will postpone for the time being the consideration of the real topography of the toothgerm represented in fig. 108.

I have observed this different behaviour of the toothgerms and their relationship to the toothband, not only in Crocodilia, but also in a number of other



Fig. 109.

Reptilia, in which I have had the opportunity of examining the earliest stages of development. It is most noteworthy that in all the cases I have studied the two types of toothgerm, which may be distinguished as "terminal" and "parietal" respectively, show a regular alternation. A terminal toothgerm is always followed by a parietal, the next in order is a terminal and so on. The following may be taken as examples of this phenomenon.

Fig. 110 represents sections through four consecutive toothgerms in the lower jaw of a young *Gecko verticillatus*. The first represents a "terminal" germ with the dentine-papilla pushed into it. Between this germ and the next a section of an interspace is shown (110 *b*). Fig. 110 *c* illustrates a section of the next germ. By comparing 110 *c* with 110 *a* two facts can be readily appreciated.

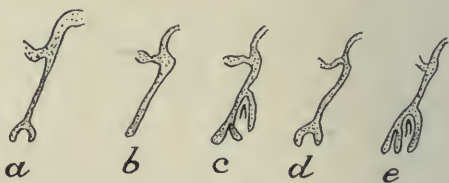


Fig. 110.

In the first place, the germ of 110 *c* is developed from the buccal side of the dental lamina which ends with a so-called free border which appears as an outgrowth on the lingual side of the toothgerm. That such a free border is formed, is easily demonstrable in fig. 109. The toothgerm in 110 *c* represents a somewhat later stage of development than that of the germ in fig. 109, but in both the dentine-papilla may be seen projecting into the buccal side of the toothband. From its earliest beginnings the lingual wall of this toothgerm is obviously thicker than its buccal. Near to the free edge of this thickened wall there appears a furrow by means of which the enamel germ becomes more completely separated from the dental lamina. The cell-mass disposed to the lingual side of this furrow, is the so-called free border of this lamina. The typographical relationship of the toothgerm to the dental lamina is obviously different in 110 *a* to that in 110 *c*. A second point worth noting is that the



parietal toothgerm of 110 *c* has attained a more advanced stage of development than that in 110 *a*, since in the former the summit of the dentine-papilla is already covered by a thin layer of hard tissue which is lacking in the latter.

An interspace intervenes between the toothgerm in 110 *c* and the next tooth 110 *d*, which is a terminal one and resembles that of 110 *a* in all respects. A third interspace follows and separates it from another parietal toothgerm 110 *e* in which the formation of dentine has commenced as in 110 *c*.

The sections shown in fig. 110 confirm the fact that in its earliest stage of development the dental lamina produces two types of enamel-organ, a terminal and a parietal, and the two types exhibit a regular alternation. The parietal germs are somewhat older than the terminal and from this it may be concluded that the formation of the former begins before that of the latter. This conclusion is strengthened by the following observations. During development the dental lamina lengthens in a backward direction, its posterior part being younger than its anterior. If the hindmost part of the toothband in a young reptilian embryo be examined the parietal germs will be found to exhibit earlier stages of development, while the terminal germs have not yet appeared.



Fig. 111.

There are other features of the posterior part of the toothband indicating that it is younger than the anterior part.

Fig. 111 illustrates another example demonstrating the two types of dental germs. In this figure sections through four consecutive germs of a young embryo of *Gongylus ocellatus* are represented. These figures are intentionally drawn on a large scale as they will be utilised for the study of the structure of the dental lamina.

These sections again supply evidence of the existence of the two types of the earliest germs produced by the toothband. It may be specially noted that the so-called free margin, in association with the parietal germ which is situated very definitely upon the buccal side of the toothband, is differentiated very early. Further the alternation of the two types is manifest.

The structure of the dental lamina will be discussed in detail later, but certain remarks concerning it may be interpolated here. A striking feature of the toothband observable in all reptilian embryos and sometimes even in very young mammalian embryos is, that it is an actual folding of the superficial

epithelium sinking into the subjacent mesenchyme. This organ consists therefore of a double lamina and is composed of an outer or buccal plate and an inner or lingual plate.

I am influenced by two reasons for laying stress upon this fact. In the first place it teaches us the real nature of the toothband and the relationships of the toothgerms. As fig. 111 clearly shows the buccal plate of the toothband alone possesses a formative function, the enamel-organs being exclusively derived from it. This is incontrovertibly the case as far as the parietal germs are concerned and is also true as regards the terminal germs. The small club-shaped thickenings, representing the earliest stages of development of these germs, appear near to, but not quite at the border of the fold. Further the dentine-papillae grow into the buccal aspect of these germs. The tooth lamina is more rightly called the toothfold, a term used by the earlier morphologists. The expression "toothband" fails to convey its true character and the German term "Ersatzleiste" is, as will be shown later, absolutely misleading.

*The two epithelial layers contributing to the dental lamina are not equivalent; the lingual layer is passive and takes no part in the formation of the enamel-organs.*

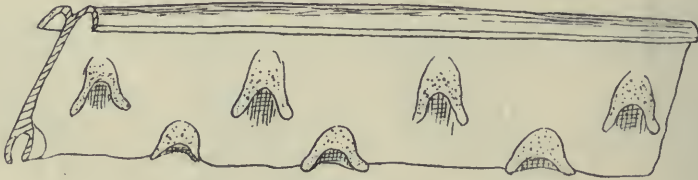


Fig. 112.

In reptiles the enamel-organ is produced by the buccal layer exclusively. This fact is of the greatest interest, since it implies a complete harmony between the dentition of the reptiles and that of the lower vertebrates, more especially of the Selachii. To this point I will revert later. I could add many more examples illustrating the same points as those given in figs. 108 to 111, but it would be superfluous to do so. The structure of the toothband in reptiles and the relationship of the toothgerm to it, as I have formulated them, are not exceptional but are the rule as may be easily verified by anyone possessing suitable material for examination.

That the toothgerms which I have termed "terminal" may be the succeeding teeth of the parietals is a question which may naturally present itself to my readers. Having made this possibility a matter of special investigation I can state definitely that, as regards tooth replacement, there is no relationship whatever between the parietal and terminal teeth.

The first fundamental fact elucidated by my researches is that in reptiles not only are there two types of toothgerm but each type is disposed in a different manner on the toothband. Fig. 112 is an attempt to represent diagrammatically a portion of the toothband of a young reptilian embryo viewed

from the buccal side and showing the arrangement of the toothgerms. This figure demonstrates that, in its earliest stage of development, the dentition of reptiles consists of two rows, the components of which alternate regularly. These rows I shall distinguish as "Odontostichi," and term the dentition as a whole "distichical." Of the two rows I name the one consisting of the parietal germs "Exostichos" as it is disposed nearer to the surface, the other consisting of the terminal germs "Endostichos." The teeth of the exostichos appear earlier than those of the endostichos, the development of the latter, as compared with the former, being always somewhat behindhand.

We must now consider how the two types of toothgerms participate in the building of the functional dentition. As far as the arrangement of the teeth upon the jaws is concerned there is no indication of the distichical character of the dentition, since the teeth are placed in a single series. When, however, the method of tooth change is closely examined the distichical character becomes apparent in a somewhat unexpected manner. Stress has already been laid upon the fact that in reptiles the endostichical teeth are not the successional teeth of the components of the exostichos. The latter are older than those of the endostichos and are situated nearer to the border of the jaw. As they move towards the surface they reach this border and attach themselves to it before the elements of the endostichos. In the meantime, as a result of the elongation of the jaw, the dental interspaces widen. Later the teeth of the endostichos fill up these interspaces, an endostichical tooth pushing itself in between two exostichical teeth at regular intervals. As a final result the functional dentition consists of a single row. This eventual monostichical arrangement is apparent only, the primitive distichy having become obscured. The exostichical and endostichical teeth alternate regularly and function simultaneously. This condition constitutes the fundamental difference between the dentitions of reptiles and of mammals respectively. As two rows of teeth both take part in its construction the dentition of the reptile may be termed "hamastichical."

I shall endeavour to prove in a subsequent essay that the marsupial dentition is also built up of two rows, but the process is incomplete and the mixing of the elements of the two rows is irregular. In order to distinguish the regular arrangement found in the reptile where a tooth of the endostichos regularly intrudes into an interspace of the exostichos the dentition of the reptile may be further defined as "isocrasie hamastichical."

To render the exposition of the developmental history of the reptilian dentition as simple as possible I have omitted one phenomenon observable in nearly all reptiles. The first teeth appearing in the embryo do not as a rule attain maturity, but calcify prematurely, lose their connection with the dental lamina, are surrounded by mesenchyme, and finally atrophy completely. This fact is only mentioned here incidentally and does not modify in the least my line of argument concerning the relationships between reptilian and mammalian dentitions. For a more complete story of the development



of reptilian dentitions I would refer the reader to a paper of one by my pupils<sup>1</sup>.

The manner in which tooth replacement occurs in reptiles may now be discussed.

In my fourth essay (*q.v.*) I showed that the teeth are produced from a matrix in a manner comparable to the development of hairs and scales, ectodermal organs which also exist temporarily and are cast off periodically. A succeeding hair or scale arises upon the same papilla as its predecessor, and is formed from the same epithelial matrix.

The succession of teeth in reptiles occurs in a similar manner. The potentiality of producing teeth is concentrated in a number of well limited areas of the toothband. Such an area I will call a tooth matrix. These matrices are anatomically indistinguishable and they consist of the same epithelial elements as those of which the whole lamina is composed. The conclusion, that such tooth matrices exist, is drawn from the fact that on the same spot on the dental lamina, where a tooth is formed a succeeding tooth appears after a longer or shorter period. Further, in some few cases the dentine-papilla of a very young tooth and that of its predecessor are not sharply separated from one another, but a slight connection exists between them. I will allow that the idea of tooth matrices is hypothetical, but in the course of this essay I hope to establish certain facts which render their existence unquestionable.

If it be admitted that the toothband is the bearer of the tooth matrices the functional significance of this band appears to be somewhat different from that generally ascribed to it. Its function is obviously to carry the tooth matrices from the surface into a deeper and more protected situation.

I have shown that the first teeth produced by the dental lamina are arranged into two rows, an exostichial and an endostichial. Combining this fact with the doctrine of tooth matrices I arrive at the following conception. In the dental lamina of the reptiles there are two rows of matrices, an exostichial and an endostichial and the components of the two rows exhibit a regular alternation.

Tooth change takes place in reptiles in the following manner. After a matrix has produced a tooth, it enters into a state of inactivity during which the tooth produced moves towards the surface and becomes attached to the jaw. This state of inactivity lasts for a longer or shorter period, but in due time the matrix again becomes active and produces another tooth. The second tooth in its turn moves towards the surface, approaches the border of the jaw and pushes out its predecessor. By a repetition of this process a tooth matrix is continually producing new teeth during the existence of the animal in precisely the same way as a scale matrix produces new scales. The total number of teeth produced by one tooth matrix is distinguished as a "tooth-family" of which each member is a "tooth-generation." A tooth is always

<sup>1</sup> M. W. Woerdeman. "Beitrage zur Entwicklungsgeschichte von Zahnen und Gebiss der Reptilien. *Archiv für mikroskopische Anatomie*. Vol. 92.

pushed out by the next succeeding generation of its own family and the two teeth are so related to one another as to be regarded as an older and a younger brother. Further, it is obvious that exostichical and endostichical tooth-families must exist in the reptile and that an exostichical tooth is only replaced by an exostichical and an endostichical tooth by an endostichical. In mammals tooth replacement is of an entirely different character.

I have defined the functional dentition of reptiles as "isoerasic," which means that the exostichical and endostichical teeth are disposed in regular alternation. How this came about has already been described; the components of the endostichos filling up the gaps left between the teeth of the exostichos. Although the characteristics of the teeth themselves do not indicate the composite nature of the dentition, yet this is not infrequently demonstrated by the peculiar way in which the teeth are renewed, viz. alternately. Very striking testimony of alternate replacement is afforded by fig. 97 (fourth essay) in which the premaxillary dentition of a full-grown *Tupinambis nigropunctatus* is represented. This dentition consists of a median tooth and five teeth on either side of the median line. On each side the successional teeth of the first, third and fifth teeth, which are on the point of corroding the fangs of their predecessors, may be seen, but of the succeeding generations following the second and fourth teeth, there is as yet no sign. This is obviously a very efficient manner of renewing the dentition and is a consequence of its distichical nature. The first teeth of the exostichos have been shown to be somewhat older than those of the endostichos. This difference is perpetuated, with the result that a new generation of the endostichical teeth will always appear somewhat later than that of the exostichical teeth. The replacement of the two types of teeth cannot therefore occur simultaneously.

In proof of this alternating tooth change I may draw attention to another fact. The process of tooth replacement is not equally intense in all reptiles. In some animals where the intervals between two tooth-generations is very short, the tooth matrices produce tooth-families rich in generations. In other animals the interval is very long and the tooth-families are poor in generations. As examples of the first type *Lacerta* and *Mabuya* may be mentioned, and of the second the genus *Calotes*. In a somewhat older embryo of the first type three or four generations in different degrees of development exist simultaneously. A horizontal section through the jaw of such an embryo demonstrates clearly that the components of one of the odontostichi are in a more advanced stage than those of the other, and that the tooth change must necessarily take place alternately.

In fig. 113, a section of one half of the upper jaw of an embryo of *Mabuya* is delineated. The maxilla (black) is cut through lengthwise and sections of the teeth are to be seen between this bone and the toothband (stippled). Close to the maxilla extends a row of five teeth, while on the lingual side of each of these teeth is its successional tooth, still in connection with the toothband. These rows represent the first and second generations of the exostichical

tooth-families. In the interspaces between the pairs of exostichical teeth are sections of endostichical teeth still partially connected with the toothband, and the replacing teeth of which have not yet appeared.

As a result of this condition of the dentition it is obvious that the replacement of the exostichical teeth must be accomplished before that of the endostichical has commenced, for the second generation of the former has already attained a rather advanced stage of development, while there is no vestige of the replacing teeth of the endostichical set. A similar condition is shown in fig. 114, which represents the front part of the upper jaw (maxilla and premaxilla) of a *Lacerta*. This embryo was somewhat older than that of *Mabuya*, since the more buccal row of teeth have already coalesced with the skeleton of the jaw. The coalesced teeth represent the first generation of the exostichos. Two such teeth are united with the premaxilla and the two alternating endo-



Fig. 113.



Fig. 114.

stichical teeth are still in connection with the toothband. Three teeth are united with the maxilla and their replacing successors (the second exostichical generation) are present. The three endostichical teeth on the other hand, although occupying the interspaces between the teeth of the first generation of the exostichos, are not yet attached to the bone. This figure illustrates the fact that as a result of the exostichical teeth being formed before the endostichical, the first generation of the exostichos attains attachment to the bones of the jaw before that of the endostichos. This figure also illustrates the way in which the endostichical teeth are intercalated between the exostichical.

The fundamental characteristic of tooth change in reptiles is that each tooth matrix produces a tooth-family, and an older member or generation of this family is continually being replaced by a succeeding or younger member. This modus of tooth change may be termed "merobolic."

The modus of tooth change in the mammal may now be examined and compared with that in the reptile.

Stress has been laid upon the fact that the dentition of reptiles is distichical, the tooth matrices being arranged in two rows. Now the fundamental point to be noticed is, that in mammals a comparable arrangement is found as the



tooth matrices are arranged in two rows the components of which alternate with one another. In mammals, however, the two rows attain a much greater independence, the row which I have distinguished as the exostichos producing the milk teeth, while the second row or endostichos is responsible for the so-called permanent teeth. That the germs of the permanent teeth and those of the milk teeth alternate is a fact which has been recognised for a very long time. This condition is inherited by the mammals from the reptiles in which it is much more evident. Another point of agreement between the two groups of vertebrates lies in the fact that in reptiles the exostichos appears before the endostichos although the interval between them is very short, while in mammals the germs of the exostichical teeth (milk teeth) also appear before those of the endostichical teeth (permanent teeth), but the interval between them is considerably longer. The reason for the retardation of the endostichos is comprehensible as the milk teeth function for a comparatively long period. In many cases, as in man for instance, this period is so long that it is difficult to understand why the germs of the permanent teeth should appear so early in the embryo. This fact, however, becomes intelligible if it is remembered that in reptiles the teeth of the endostichos participate at one and the same time with those of the exostichos in the construction of the functional dentition, and a nearly simultaneous appearance of the teeth of both rows is a necessity. The mammals have inherited the potentiality of a hamastichical dentition from their reptilian ancestors, and although the interval between the appearances of the two sets of teeth is prolonged yet the two sets of germs both appear early.

Having traced the fundamental harmony existent between the dentitions of the reptiles and the mammals, points of difference between the two may now be considered.

As they grow towards the surface the endostichical teeth of the reptile become sandwiched in between the elements of the exostichical row to form with them a single row of teeth. In mammals, on the contrary, the exostichical teeth (milk-set) after becoming implanted into the bones of the jaws, form a continuous series which is retained for a longer or shorter period. In some animals they are absorbed before birth, in others they persist until the animal is full grown. During this period the endostichical teeth (or permanent teeth) undergo further development but remain hidden under the gums until the succession of teeth begins. Consequently the essential character of the mammalian dentition is that the two rows of teeth are functionally independent. The functional dentition consists either of teeth belonging to the first row or of those belonging to the second, both rows functioning successively and not simultaneously as is the case in the reptiles. In contradistinction to the hamastichic dentition of reptiles I term the dentition of mammals "chorisstichic." When the mammal attains the age when teeth-succession occurs an element of the milk-set (an exostichical tooth) is replaced by one of the permanent set (endostichical tooth). The fundamental difference between tooth-

succession in mammals and reptiles can now be defined. In reptiles a tooth is replaced by the succeeding generation of the tooth-family produced by the matrix from which the first tooth was derived (merobolic tooth-change). This process may be repeated as often as the matrix is capable of forming a new member of the family and is practically unlimited. In mammals, on the contrary, a tooth of the exostichos is replaced by one of the endostichos and since the activity of the tooth matrices is condensed into a single production, the whole tooth-family being concentrated into one complicated tooth (*vide* Essay IV) tooth change can only occur in this group but once. In mammals tooth change is a succession of one tooth row after another: in reptiles it is a succession of tooth-generations. The two processes though apparently identical are fundamentally different. In contradistinction to the process in reptiles, which I distinguished as "merobolic," I will denominate that in mammals as "stichobolic."

My contention that, to derive the diphyodontism of mammals from the polyphyodontism of reptiles is a scientific mistake, can now be appreciated, as the difference between the two is not one of quantity but one of quality. In order to render my views intelligible, I have devised two schemes (fig. 115) illustrating the mode of tooth-succession in reptiles and mammals respectively. In scheme "a" six tooth-families of a reptile are represented, three belonging to the exostichos (white) and three to the endostichos (striped), four generations of each family being present. The modus of tooth succession is indicated by arrows. In scheme "b" the replacement of teeth in mammals is represented, three exostichical teeth (white) and three endostichical teeth (striped) are sketched. The modus of replacement is again indicated by arrows. The two schemes require no further explanation, as they illustrate very clearly the difference between the merobolic succession of reptiles and the stichobolic succession of mammals.

Scheme "b" presents the view regarding the origin of mammalian teeth which I expounded in my fourth essay and thus the two great odontological problems: (1) the origin of the composite mammalian tooth and (2) the true interpretation of tooth replacement in mammals are brought into line with one another. The two problems have the closest bearing one upon the other, since my theory as to the manner in which the composite tooth of mammals has arisen is incompatible with the view that tooth replacement is comparable with that which occurs in reptiles. In reptiles tooth-succession consists in the replacement of an older generation of the tooth-family by a younger. In mammals the whole tooth-family being concentrated into a single composite

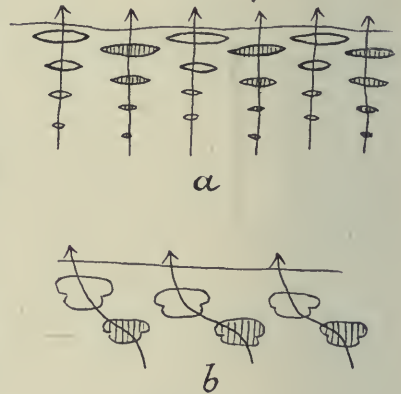


Fig. 115.

tooth, an entirely new form of tooth-succession must have been acquired. The close correlation between tooth-origin and tooth-succession in mammals is responsible for the plea I advanced in my fourth essay, that criticism of my theory concerning tooth-origin be suspended until my views on tooth-succession had been formulated.

In that essay I defined what I understand by a tooth matrix. In both reptiles and mammals the tooth matrices are arranged in two rows, the components of which exhibit a regular alternation. In reptiles a matrix first produces a tooth, after a shorter or longer interval a second tooth, then a third and so on. During the lifetime of the animal the matrix produces a tooth-family of more or less abundant individuals, an older generation being successively replaced by a younger. This is possible because the members of the family are to all intents and purposes independent of one another and possess a simple form. In the mammals the productivity of the tooth matrix is limited to two generations, owing to the process which I have described in the foregoing essay as tooth concentration whereby the two generations coalesce, the result being a tooth of complicated form (dimer). Thus, the so-called polyphyodontism of reptiles is condensed into the complicated tooth form of the mammals and the diphyodontism of mammals is necessarily a phenomenon of an entirely different nature. I would further emphasise that owing to the structural principle of the dentition inherited by the mammals from their reptilian ancestors, namely, the distichical arrangement, the acquirement of the new modus of tooth change in mammals was rendered possible.

I submit that my theory marks an advance in the morphological understanding of the teeth, as it brings the two principal problems of odontology into logical sequence one with the other and their solution is attained on one common basis.

From the point of view of my theory the doctrine of prelaeteal and post permanent dentitions falls to the ground, as it is incompatible with my conceptions. The possibility of such dentitions can only be allowed if the diphyodontism of mammals be regarded as a process identical in nature with the polyphyodontism of reptiles, the difference between the two being purely quantitative. In such case it is justifiable to enquire whether or no there are traces in mammals of tooth-succession preceding or succeeding the two normal dentitions. As according to my theory, the process of tooth-succession in mammals is fundamentally different from that in reptiles, the replacement of teeth being due to a succession of rows, and further, as there are only two such rows (exostichos and endostichos) tooth-succession can only occur once and the possibility of prelaeteal or post permanent dentitions falls outside the range of discussion.

Many appearances regarded as traces of a prelaeteal or a post permanent dentition have been described and naturally require some explanation. In my second and third essays certain phenomena which I had observed during



my investigation upon the development of the mammalian teeth were described. In order to avoid recapitulation I may here state briefly that the whole complex of phenomena described and interpreted in mammals as traces of a prelaeteal dentition are in reality either rudiments of the tooth gland-lamina of reptiles (Essay III) or fragments of the lateral enamel-band of mammals (Essay II). If the significance of these formations had been more generally appreciated the doctrine of a prelaeteal dentition would never have attained the importance it has in odontological literature.

As concerns a supposed post permanent dentition I will confine myself at present to a simple denial of its possibility. Some investigators consider the so-called free-border of the dental lamina indicates a post permanent or third dentition. I am convinced that this is an error, but I will reserve its discussion for my next essay where its true nature will be demonstrated and it will become evident that my opinion coincides to some considerable extent with that advanced by Wilson and Hill in their investigation upon the dentition of *Perameles*<sup>1</sup>.

The great importance of the distichical nature of the dentitions both of reptiles and of mammals and of their relationships one to the other has, I trust, been adequately demonstrated. The way in which distichy had origin may now be discussed. The question resolves itself into whether the distichical character of the dentition was acquired by the reptiles as a group or was inherited by them from still more primitive ancestors. An examination of the dentitions of the *Selachii* not only makes the structure of the reptilian dentition intelligible, but also throws light upon the true nature of the dental lamina in the higher vertebrates. Two views regarding the development of the dentitions of the *Selachii* have been promulgated. The older, and in my opinion the correct view, is that of Owen, the other is advanced by Hertwig. It is a matter of regret that, considering they have not been substantiated by research, the views of the latter author meet with such general acceptance. As a consequence the real nature of the dental lamina has remained unrecognized ever since Hertwig bestowed upon it the most inappropriate name of "successional-band" (*Ersatzleiste*).

In Tome I of his *Odontography*, Owen states that the successional teeth of *Plagiostoma* are situated on the inner side of the jaw and are protected by a mucous fold. According to his opinion these teeth arise from free papillae occupying a furrow in the mucous membrane of the mouth and are not enclosed by an enamel-organ. The lingual wall of this furrow has the character of a "thecal lamina" and the epithelium of the inner surface of this covering fold is continued at the bottom of the groove into the tooth-forming epithelium of the outer wall. "The anterior lamina of this fold which from its office may be termed 'thecal' is continuous with the mucous membrane at the base of the rows of teeth" (*l.c.* p. 35).

<sup>1</sup> J. T. Wilson and J. P. Hill. "Observations on the Development and Succession of the Teeth in *Perameles*." *Quart. Journ. of Microsc. Sc.* Vol. XXXIX. 1897.

The essential feature of Owen's view is, that the teeth develop upon free papillae which being practically situated on the surface are protected by an overlapping fold of mucous membrane. If this fold be retracted it is at once apparent that the teeth are really situated on the surface. Hertwig's conception, on the other hand, is that a solid band grows from the surface epithelium into the subjacent mesenchyme and that the teeth are formed on the free border of this band. Hertwig asseverates that the mucous fold of Owen is an artefact invented by him in consequence of his researches being limited to the younger teeth. Hertwig's assertion is, without any reasonable doubt, fallacious and I am convinced by the results of my own investigations that Owen is right as the following summary of the phylogeny of the toothband

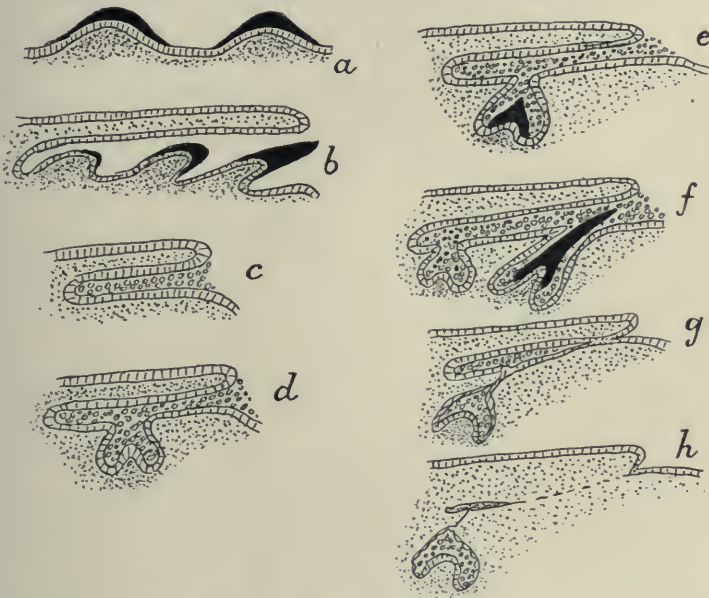


Fig. 116.

will show. The developmental scheme is illustrated by the diagrams in fig. 116.

That the teeth of Selachii are to be regarded as highly specialised dermal denticles is a generally accepted view. These denticles, the so-called placoid scales, are epithelial formations arising upon free papillae. In the first diagram of fig. 116 the position of such scales is represented. In rays and some sharks the relationship between scales and teeth is easily ascertained since there is a direct continuity between the two at the borders of the jaws, the former gradually merging into the latter. Fig. 117 shows another example of this relationship. It represents a part of the dentition of a *Selache maxima*. In this shark the dentition consists of very small teeth definitely situated on the surface and investing the borders of



Fig. 117.

the jaws. These teeth and the dermal denticles of the shark are practically identical in structure.

A further phase of development found in the majority of other sharks is shown by the second diagram of fig. 116. In *Selache* the whole complex of teeth is exposed on the surface; but in other sharks the young teeth are protected by a mucous fold derived from the lining membrane of the mouth. This fold covers the developing teeth and I shall therefore term it the "Operculum dentium" or, in short, the "operculum," while the region of the surface membrane from which the teeth are derived will be distinguished as the "toothfield." The difference between rays and the majority of the sharks is that in the former the toothfield lies freely exposed on the surface being visible for its whole extent, while in the latter, on the contrary, the toothfield, with the exception of a narrow zone bearing the teeth actually functioning, is covered over. Nevertheless in the latter the teeth are to all intents and purposes situated on free papillae of the surface as is the case in the rays, since the deep surface of the operculum is not adherent to the toothfield from which it may be easily retracted thereby fully exposing the complex of developing teeth. It must be obvious to the reader that the formation which I distinguish as the "Operculum" is identical with the "Thecal fold" of Owen and that my conception of the anatomy of the Selachian dentition agrees, as far as this feature is concerned, with that advanced by him.

Another fact to which I would draw attention, as it indicates an important advance in the development of vertebrate dentition, is that in sharks the origin of the teeth is not autonomous. This is demonstrated by fig. 116 *b*, where a furrow is to be observed between the operculum and the toothfield. At the bottom of this furrow the epithelium on the deep aspect of the operculum becomes continuous with the epithelium of the toothfield. The matrices responsible for the production of the teeth are disposed along this line of epithelial reflexion. As a tooth enlarges it migrates towards the border of the jaw, and after a longer or shorter pause, the matrix from which it was derived produces a second tooth, and so on. In fig. 116 *b*, three tooth generations all derived from the same matrix and exhibiting progressive stages of development are shown. The totality of all the teeth having origin from one and the same matrix I have previously termed a tooth-family. In sharks a number of generations or members of such a family are always found under cover of the operculum.

Sharks often furnish very conclusive evidence of my contention that the teeth of the vertebrates are not autonomously arising organs but are produced from a matrix. Disposed between tooth-families whose members are normal in shape a family of teeth exhibiting some anomalous form may appear. Fig. 118 represents the mandibular dentition of a young *Spinax niger*, with five tooth-families, each consisting of four generations at least. The teeth are tricuspidate with a long sharp central cusp on either side of which are two smaller cusps. In addition to the families all the teeth of which are normal, there is one



family whose members without exception present a duplicated main or central cusp. Such a phenomenon is unintelligible unless it be conceded that all these anomalous teeth are produced from one and the same matrix, which for some reason or another, must have undergone some modification in structure and function.

Another case illustrating a similar condition is given in fig. 119, which represents a part of the dentition of *Cephaloptera giorna*. The teeth of this shark are very small and the sharp extended edge of each tooth is serrated exhibiting five little cusps. Between the normal families is one whose members are double the length of and are provided with twice as many cusps as the normal tooth. I am quite convinced that if the dentitions of a great number of sharks were examined examples of similar cases would be easily found. Such cases leave little room for doubt that in sharks—and consequently in reptiles also—the teeth are derived from special matrices.

With this digression the developmental history of the toothband may now be further considered. In fig. 116 *c* a further stage of development is repre-



Fig. 118.

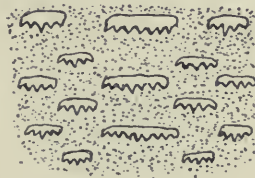


Fig. 119.

sented. The toothfield and the operculum may still be recognised. If it be compared with fig. 116 *b* it will be noticed that it has progressed in so far that the furrow between the operculum and the toothfield is now filled up with cells forming a connecting medium between the two.

In this stage a real toothband consisting of two epithelial layers separated from one another by a layer of indifferent cells may be described. The two epithelial laminae however, are far from being equivalent, as one, homologous with the toothfield of sharks, is alone concerned in the production of teeth, while the other which represents the lining epithelium of the operculum is inactive as far as tooth formation is concerned.

Figs. 116 *d*, 116 *e*, and 116 *f*, represent three stages of tooth development in reptiles. The toothband is again composed of two epithelial laminae; the toothfield-lamina and the operculum lamina which are attached to one another by an intermediate layer of indifferent cells. The toothgerms are formed exclusively from the toothfield-lamina, and the enamel-organ is in direct communication with the layer of indifferent cells filling up the interior of the enamel-organ, where they are differentiated into the well-known reticulum or enamel-pulp.

As soon as the hard tissue of the tooth is sufficiently developed, the tooth begins to push its way between the two laminae of the toothband, as is shown in figs. 116 *e*, and 116 *f*. A comparison of the figs. 116 *b*, and 116 *f*, shows the fundamental agreement between the dentitions of sharks and reptiles. In the reptile, however, the real toothband has appeared as a result of the fusion of the operculum and the toothfield, the latter sinking to a certain extent into the underlying tissue.

The open enamel-organ together with a continuity between the enamel-pulp cells and the cells of the intermediate layer of the toothband are characteristic of a great number of reptiles, in which the enamel-organ never loses its connexion with the dental lamina. Nevertheless, in one group of these vertebrates, viz. the Crocodilia, evolution as concerns both the toothband and the enamel-organ is markedly progressive. In these animals, as may be seen in fig. 116 *g*, the layer of intermediate indifferent cells is not well developed in the toothband in which the operculum and toothfield epithelial layers are, more especially near the surface, in close proximity with one another. Not infrequently the continuity of the toothband with the superficial epithelium is actually interrupted. This occurs in older embryos in which, as a consequence, the toothband is isolated from the surface and is buried in the mesenchymatous tissue. In this respect the crocodiles approach the evolutionary stage peculiar to mammals. The two groups of vertebrates are also alike as regards the enamel-organ. In lower reptiles this organ is in close connexion with the epithelial lamina of the toothband, identical with the toothfield epithelium of sharks. In crocodiles the attachment of the toothgerm to the toothband diminishes and the enamel-organ becoming more and more independent is eventually connected to the toothband by a narrow strand of cells. Finally the enamel-organ is detached from the band and becomes completely surrounded by mesenchymatous tissue, some isolated patches of epithelial cells between the band and the organ testifying to the original continuity of the two.

Setting aside these more advanced stages of evolution by which the crocodiles approach the mammalian conditions, stress must be laid upon the fact that in crocodiles the enamel-organ is produced exclusively by that component of the toothband which is identical with the epithelium of the toothfield in fishes while the component corresponding to the original lining epithelium of the operculum takes no part in the formation of the toothgerms.

The conditions met with in crocodiles enable us to understand those in mammals. In the latter group, the toothgerms are also produced by the epithelium corresponding to the original toothfield, being always formed upon the outer or labial aspect of the toothband. In reptiles the toothband becomes detached from the superficial epithelial layer more completely and at an earlier stage; further, early and complete detachment of the toothgerm from the toothband also applies. Very young embryos of some mammals demonstrate very clearly the primitive structure of the toothband consisting, as it

does, of an inner lamina (the primitive opercular epithelium) and an outer lamina (the primitive toothfield epithelium), a layer of indifferent cells intervening between the two. In some cases I have observed a characteristic difference in shape of the cells of the two laminae, those of the inner lamina being more flattened as compared with those of the outer. However, these primitive features commonly disappear very early.

This summary establishes the view that the phylogenetic history of the toothband is in reality very simple, and that a true conception of the real nature of this band is only possible after a survey of all the phylogenetic facts. The evolution of this band commences with the overlapping of the toothfield by the operculum in sharks. The ontogeny of mammalian dentition is based upon this phylogenetic process although its earliest stages cannot be observed. This primitive phylogenetic stage is often discernible however, in reptilian embryos as is demonstrated in figs. 120 and 121. In fig. 120 a section is drawn through the third tooth of the upper jaw of a young embryo of *Gongylus ocellatus*. A true toothband is not yet formed, but a broad shallow furrow filled up with intermediate cells is present. On the buccal side of the furrow a papilla arises and its similarity to the free papillae of the early dentition of



Fig. 120.



Fig. 121

sharks is very obvious (cf. fig. 116 b). Fig. 121 represents a section through the same tooth of a somewhat older embryo, and in this the formation of the hard tissue has commenced. It shows very clearly that the mucous membrane lining the mouth is disposed in the form of a fold which is beginning to overlap the young tooth. This fold is obviously the operculum.

The phylogenetic history of the toothband teaches us that its denomination by Hertwig as "successional band" (Ersatzleiste) is quite incorrect since the band had origin, not as an ingrowth of the superficial epithelium into the subjacent tissue, but as a result of the overlapping of the teeth-forming zone by a fold of mucous membrane. Tooth-succession is not associated with the band in its entirety, but only with one of its components, namely with that correspondent to the epithelium of the primitive toothfield. The true character of the band is only intelligible if it is considered as a result of a process of opercular formation.

Having established the phylogeny of the toothband, the question as to the origin of the peculiar construction of the reptilian dentition can now be discussed. A fundamental feature of the dentition is the fact that the first reptilian teeth are arranged in two rows or odontostichi on the buccal side of



the dental lamina, and that the elements of the two rows alternate with one another. This condition I distinguished as distichy. Assuming that the buccal lamina of the reptilian toothband is identical with the toothfield of the sharks, an idea as to the manner in which this distichy came about can be conceived. In order to do this the structure of the selachian dentition must be carefully examined.

Fig. 122 represents a part of the mandible of a *Carcharias glaucus*, as seen from the outer side. If the arrangement of the functional teeth set upon the

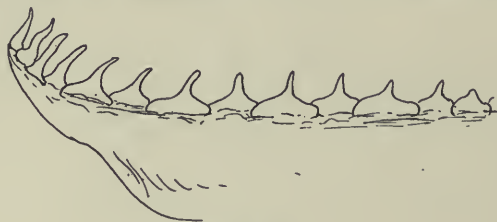


Fig. 122.

border of the jaw be examined, it is obvious that they are disposed in two rows, an outer and an inner, the components of the two rows exhibiting a regular alternation. The similarity of the arrangement to the reptilian dentition is very striking, since the latter is built up from two rows of teeth derived respectively from endostichical and exostichical teeth matrices. There is however one important difference. The primitive distichical character of the functional teeth in reptiles is obscured in that the teeth of the inner row are intercalated regularly between those of the outer row. In *Carcharias* on the contrary and apparently in other sharks as well, this intercalation does not take place and the distichical character is manifest.



Fig. 123.

By examining the inner side of the jaw, where the replacing teeth are still lying recumbent, it is evident that this distichical arrangement of the functional dentitions will persist. In fig. 123 a part of this dentition exposed by removing the operculum is sketched. As in reptiles it consists of a number of tooth-families there being no difference between the construction of the selachian dentition and that of reptiles. The existing members of each selachian tooth-family may however be more numerous than those in reptiles. This circumstance is due to the fact that in sharks the process of tooth change has greater intensity than that in reptiles. I would draw special attention to the alternating positions of the members of the tooth-families.

Not only does the construction of the reptilian dentition agree with that of sharks, but the factor determining distichical arrangement of the former can be appreciated if it is realised that the selachian dentition is so arranged in parallel rows that the component elements of one row alternate with those in an adjoining row.

Consequently the distichical character of the dentitions of mammals and reptiles is inherited from very primitive ancestors, in which it was simply a retention of an arrangement characteristic of the skin investment of the animal. In reviewing all these facts and keeping especially in mind that tooth change in mammals is a succession of tooth rows (and not, as in reptiles, a succession of tooth-generations) the following somewhat surprising conclusion can be drawn. *The modus of tooth change in mammals is based upon the arrangement of the dermal denticles of the skin in primitive vertebrates.*

# A FOETUS PRESENTING A COMBINATION OF RARE ANOMALIES

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THE investigation of the interdependence of the various processes of growth is attracting less attention than the search for evidence of the interdependence of the various physiological processes in the circulatory, excretory and endocrine systems. It therefore seems advisable to analyse all monsters with a view to ascertaining the extent of "action at a distance" in the various processes of growth. This attitude is the justification for the following description of a male foetus miscarried in the twenty-seventh week of pregnancy by a primiparous woman of 25 years of age. The foetus presented as a breech in the unruptured bag of membranes. The placenta was retained for one hour and its separation was followed by a sharp post-partum haemorrhage. The general health of the mother was good before and during pregnancy, and there was no history of a previous miscarriage. The paternal and family histories yielded nothing of note.

## EXTERNAL FEATURES

The foetus had been dead for some days *in utero*, and its macerated condition unfortunately interfered with histological examination. The length from crown to rump is 16 cms., and the weight is 400 grams. The subcutaneous fat and muscles are badly developed and the left half of the thorax appears to be markedly collapsed. The umbilical cord displays but one artery and one vein, a condition which is usually associated with some degree of symphodia (Ballantyne '04, Dawson '22), but which, in this case is associated with a right club-foot. The left arm is very short and presents only two fingers. The head and its apertures appear normal, but there is no trace of the anus or post-anal dimple, the median raphe extending from the tip of the coccyx to the base of the penis, which, with the scrotum, is normally developed for seven months.

## X-RAY EXAMINATION

The vertebral column is decidedly irregular (fig. 1), the marked scoliosis being accompanied by malformation of the eighth and ninth dorsal vertebrae, which are wedge-shaped and exhibit single asymmetric centres of ossification for the centra. The upper seven dorsal vertebrae present double centres symmetrically placed and the third sacral presents a single asymmetric centre. The centres of ossification for the neurocentral arches are normal except in



the case of the eighth and ninth left dorsal arches, where they are suppressed, and the sixth and seventh left, where they are fused. The ribs on the right side are normal, but on the left side the eighth and ninth ribs are wanting,



Fig. 1. Radiogram of the Foetus.

and a first lumbar rib is present; moreover, varying degrees of fusion have occurred between the third, fourth, and fifth, the sixth and seventh, the eleventh and twelfth, so that posteriorly the eleven ribs are distributed over thirteen vertebrae, whereas anteriorly the number is apparently reduced to

eight ribs, the first to the seventh being vertebro-sternal, the tenth to the twelfth vertebro-costal, and the thirteenth floating. The sternum displays centres of ossification in the three upper segments, a degree of ossification which is normal for the seventh month of foetal life.

The left upper limb has a short humerus, no radius or ulna, and two metacarpals with three phalanges apiece. There is a trace of a more radial metacarpal, but no phalanges are attached thereto. The centre of ossification for the body of the pubis has not appeared and the right foot is clubbed, the deformity being concentrated at the neck of the astragalus. The centre of ossification for the os calcis is present.

#### A. THE VERTEBRAL COLUMN AND RIBS

Ossification normally commences in the neuro-central arches (hemi-arches) of the cervical vertebrae about the seventh week of foetal life, and, extending caudally, reaches the region of the third sacral vertebrae about the seventh month. Ossification commences in the centra of the lower dorsal region about the seventh week, and, extending cranially and caudally, reaches the odontoid process at the fourth month and the fifth sacral vertebra at the fifth month. In the ribs, ossification takes place a few days ahead of ossification in the vertebrae, commencing in the seventh rib and spreading cranially and caudally (Pinkus '10, Keith '21). The extent of the anomalous development in the vertebrae and ribs of this foetus is shown in the radiogram (fig. 1) and in the diagram constructed therefrom after dissection of the vertebral column (fig. 2). Perhaps the most interesting feature is the condition presented by the eighth and ninth thoracic vertebrae, in which the left half of the vertebrae is suppressed.



Fig. 2. Diagram of dorsal, lumbar and sacral portions of vertebral column.

The first record of deficiency of a half vertebra appears to be that of Rokitsansky (1842), who regards the deficiency as a well-recognised cause of scoliosis. On the other hand, Struthers, in his description of vertebral variations (1875) does not mention absence of half a vertebra. In the same year Goodhart reports cases of deficiency of a half vertebra and cases of "doubling" of the centrum. Brash (1914-15) gives a summary of the literature previous to and after the advent of X-ray diagnosis and points out that there is a dearth of post-mortem corroboration of those cases of scoliosis which have been attributed to this cause. The most comprehensive studies of the anomalies of the vertebral column are those of Joachimstal ('10) and Falk ('20).

In the recorded cases of vertebral anomalies there are but few references to the ribs. Goodhart (1875) records the case of an adult with the whole of the first lumbar, the left half of the twelfth thoracic, and the right half of the second lumbar vertebrae wanting, with the existence of a thirteenth rib on the left side. Willet and Walsham (1880) record a case of deficiency of four and a half vertebrae in the upper dorsal region, the fourth left and fifth right ribs being wanting. Bolk has described a human skeleton showing bifurcation of several ribs and a number of small bones intercalated between the laminae in the dorsal region of the spine. Falk (1920) describes several cases of deformities of the ribs associated with malformation of the vertebral column and quotes Putti as follows:—"Since the rib is to be regarded as a product of the ventral portion of the hemi-arch, the costal anomaly of the thoracic skeleton is always inseparably bound up with a vertebral anomaly, so that in a lack of the costal element, either a half vertebra or at least the ventral portion of the hemi-arch is missing. Also in fusion of the ribs, a sign of irregular segmentation exists in the vertebra."

An analysis of the cases of suppression or intercalation of a half vertebra shows that there is a site of maximum frequency. The condition has been observed from the third cervical to the third sacral region, fifty per cent. of the cases occurring between the eighth dorsal and first lumbar. As regards doubling of the centres, this is still more marked, as ninety per cent. of the cases occur between the first and ninth dorsal vertebrae. Ever since von Baer (1837) called attention to the asymmetry of the embryonic axis in relation to the yolk sac, various mechanical factors with marked bending, wrinkling or torsion of the embryonic axis have been invoked to explain skeletal anomalies. Jansen ('21) maintains that the stress of increased amniotic pressure in the precartilaginous (sclero-blastemous) stage of the embryo, when the amnion lies dorsal thereto, falls on the cervical and lumbar regions, leading to anencephaly and spina bifida. During the early cartilaginous stage when the amnion surrounds the embryo, the stress falls on the head, lumbo-dorsal column, and extremities, leading to achondroplasia (Jansen) and mongoloid idiocy (Van der Scheer '18). Brash ('14-'15) records the case of a man with an absent half vertebra who served in the army and was free from marked deformity. The protagonists of excessive amniotic pressure have not described frequent vertebral anomalies, other than kyphosis in the cases of achondroplasia and mongoloid idiocy. Thus the limitations of the mechanical theory are evident.

Falk rejects the various mechanical theories and attributes the condition to a defect of the primitive segmentation. It is evident that the problem must be examined anew in terms of the evolution of skeletal segmentation, and for this reason all cases of vertebral and costal irregularities, especially those ascertained in the course of routine X-ray examination, should be recorded.



## B. THE THORAX

The thymus is small and fails to cover any portion of the pericardial sac. The heart is displaced to the left and upwards so that the right border lies behind the right half of the sternum and the apex reaches the anterior border of the axilla in the third intercostal space. The pericardium is adherent to the antero-lateral portion of the collapsed thoracic wall up to the level of the second intercostal space. The right lung is normal, but the left lung is absent. There is no trace of a left pleural cavity as the pericardium is loosely adherent to the costal parietes. The dome of the left half of the diaphragm ascends posterior and lateral to the pericardial sac and is closely applied to the postero-lateral aspect of the chest wall to the level of the third rib, loose areolar tissue intervening. The left wall of the pericardial sac contains numerous muscular fibres supplied by twigs from the left phrenic nerve.

The presence of muscular fibres innervated by the phrenic nerve in the left wall of the pericardium, the contiguity of the left half of the diaphragm and the costal parietes up to the level of the third rib space, together with the absence of the left pleural cavity and lung is of great importance in connection with Keith's ('05, '10) description of the rôle played by the rectus abdominis and transversalis sheet of muscle in the formation of the diaphragm. I hope to discuss the significance of the condition here met with in a further contribution dealing with two atypical cases of diaphragmatic hernia.

The oesophagus is definitely interrupted at the level of the seventh cervical vertebra (fig. 3). The larynx and cervical trachea are normal but the bifurcation of the trachea presents a striking anomaly. The right bronchus leads to the right lung, but in place of the left bronchus is a small canal of 1 mm. diameter, lined with epithelium, which passes downwards for 8 mm. to become continuous with the distal portion of the oesophagus at the level of the sixth dorsal vertebra (fig. 3).

Tracheo-oesophageal and broncho-oesophageal fistula with stenosis of the proximal part of the oesophagus has been frequently reported. Comprehensive studies of the condition have been published by Morell Mackenzie (1884), Happich ('05), Forssner ('07), Giffhorn ('08), Phillips ('08) and Keith ('10). Three characteristics are afforded by the cases described; firstly, the large number of associated abnormalities such as imperforate anus, pulmonary stenosis, club foot, spina bifida and right aortic arch; secondly, the limitation of the stenosis of the oesophagus to the site of junction of two morphological portions of the oesophagus, the para-tracheal and retro-tracheal portions of Keith; thirdly, the site of origin of the tracheo-oesophageal fistula from the dorsal wall of the trachea near its bifurcation. Forssner and Keith attribute the condition to the lateral margins of the distal portion of tracheal groove uniting on the dorsal wall of the gut instead of in the ventral wall.

The lung anlage of the 2.5 mm. embryo and of the 4.25 mm. embryo (Rob. Meyer) is definitely unpaired. In the 4.9 mm. embryo (Hertwig) and

5 mm. embryo (Rob. Meyer) the trachea is definitely divided off from the oesophagus and the right and left lung buds are developed; the right lung bud is the larger and is directed caudally, while the left has an almost transverse direction. In the 4 mm. embryo Broman shows in addition to the tracheo-oesophageal septum which is as yet not separated off, a lateral



Fig. 3. Stenosis of the oesophagus with tracheo-oesophageal fistula. *Tr.* trachea; *Oe.* oesophagus; *F.* fistula; *CC.* common carotid; *Ao.* aorta; *S.* subclavian; *V.* vertebral artery.

oesophageal groove which causes the oesophagus to be a narrow antero-posterior figure 8 on cross-section. Obliteration of the posterior lumen of the figure 8, with persistence of the communication between the anterior lumen of the figure 8 and the trachea would lead to the condition which is being discussed. This has been suggested by Lewis ('12).

Keith and Spicer have described three consecutive cases of stenosis of the

oesophagus with persistence of that abnormal right subelavian artery which passes dorsal to the oesophagus, and have attributed some function to this portion of the fourth right dorsal arch in the production of the deformity. This explanation is not warranted, as in the 4 mm. embryo, which is close to the stage at which the deformity must arise, the fourth branchial artery is in relation to its branchial pouch and the dorsal aortae fuse in the neighbourhood of the second cervical segment. Similarly in the case under discussion the position of the tracheo-oesophageal fistula in relation to the left aortic arch (fig. 3) does not exist throughout development, as the elongation of the oesophagus takes place much more rapidly and to a far greater extent than the migration of the arches. The absence of the left bronchus and lung makes this case quite different from any of the fourteen cases collected by Keith ('10) from the Museums of the Royal College of Surgeons and Metropolitan Medical Schools.

### C. THE HEART AND GREAT VESSELS

The apex of the heart is bifid, and the ventricular septum is complete. The walls of the auricles are thin and the auricular septum is deficient, being represented by a few strands of tissue which cross the cavity on the posterior wall. The auriculo-ventricular, aortic, and pulmonary valves are normal. The Eustachian valve guarding the entrance of the inferior vena cava is normal, but the Thebesian valve guarding the entrance of the coronary sinus is larger than normal, the opening of the sinus being larger than the opening for the inferior vena cava. The auricular walls average 0.5 mm. in thickness and the ventricular walls 2.5 mm.

The bifid apex is a condition which may appear with or without grave anomalies, and is normal to the dugong. In the 5 mm. embryo, when the primary auricular and ventricular septa are forming, rapid downgrowth of the apices of the ventricles takes place so that the interventricular groove is distinct. Obliteration of this deep groove takes place in the 11 mm. stage by development downwards of the embryonic apex (Abbott '15). Mall ('12) maintains that persistence of the bifid apex is due to absence of the muscular vortex normally present at the apex. A deeply bifid apex occurred in three of Thérémis's 106 cases, and in four of Abbott's 631 cases of abnormal hearts.

The auricular septum in this heart is represented only by a few strands which cross the cavity in the dorsal wall, so that the heart is virtually a case of "cor biventriculare." It is probable that this is an example of a huge persistent ostium secundum (foramen ovale) which has escaped closure through failure of development of the septum secundum. Such an anomaly is rare and points to the possibility of a disturbance occurring after the appearance of the septum primum (4 mm. stage) and before the appearance of the septum secundum (8 mm. stage).

In a series of 631 cases, Abbott reports 14 cases of rudimentary auricular



septum and five cases of complete absence, and states that persistence of the left superior vena cava belongs to the same complex.

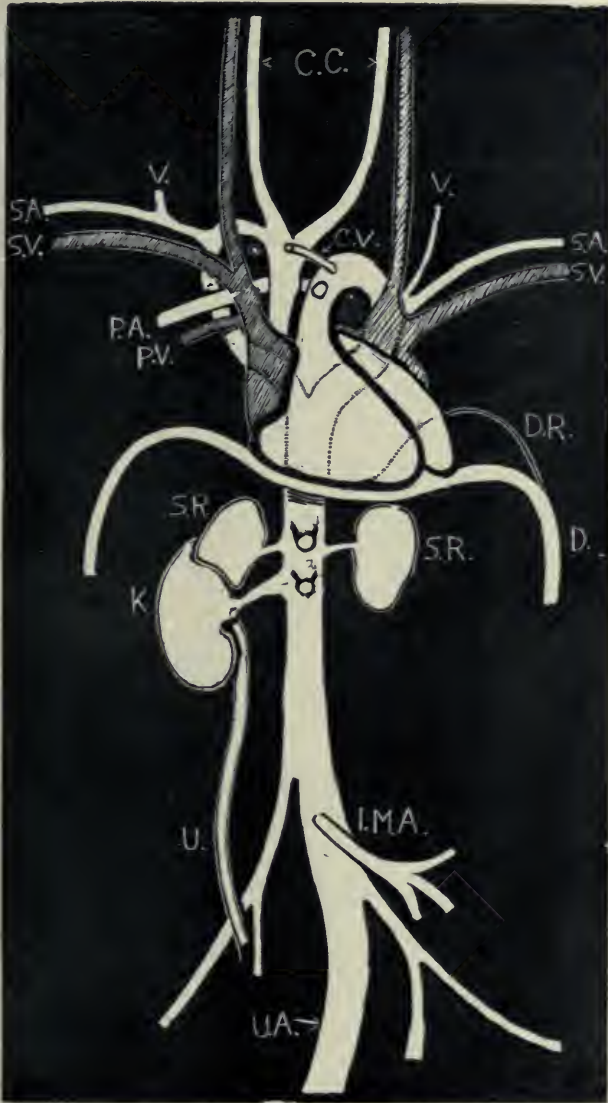


Fig. 4. Circulatory system. *C.C.* common carotid; *S.A.*, *S.V.* subclavian artery and vein; *P.A.*, *P.V.* pulmonary artery and vein; *D.* diaphragm; *D.R.* diaphragmatic recess postero-lateral to pericardium; *S.R.* suprarenal; *K.* kidney; *U.* ureter; *U.A.* umbilical artery; *I.M.A.* inferior mesenteric artery;  $\odot$  recurrent laryngeal nerves; *C.V.* vessel communicating posterior aspect of the two systemic arches. The vessel is shown anteriorly for clearness.

The internal jugular and subclavian veins of the right side form a vena cava superior which enters the right auricle. The corresponding vessels on the left form a vena cava superior which passes anterior to the left systemic

arterial arch to form a dilated coronary sinus which enters the right auricle. The fused pulmonary veins from the right lung enter the left auricle as a single trunk near its upper border. The inferior vena cava and azygos system are normal. The phrenic and vagus nerves are also normal in their course and relations in the neck and thorax.

The anomaly presented by the great veins is due to a persistence of the embryonic left superior vena cava and left duct of Cuvier with consequent replacement of the coronary sinus. This arrangement is normal in many mammals (Robinson '17). The left superior intercostal vein entered the left superior vena cava and the great cardiac vein entered the coronary sinus, but there was no trace of a left vena azygos major, neither was there a left lung root to assist in the task of ascribing any definite rôle to any minute anastomosis. The anastomosis between the left and right superior venae cavae in the neighbourhood of the thymus was not well marked.

The great arteries of the thorax present a condition hitherto undescribed. From the left ventricle (fig. 4) arises a right systemic arch which runs upwards and slightly to the right, arches backwards over the root of the right lung, and gives off in turn the left carotid, right carotid and right subelavian vessels. From the right ventricle ascends a left systemic trunk which is anterior and to the left of the vessel arising from the left ventricle. As it arches upwards and to the left it gives off a right pulmonary artery which passes dorsal to the ascending portion of the right systemic arch; it then continues as a well-defined arch, gives off the left vertebral and left subelavian arteries, and descends to join the right arch to form the descending aorta at the level of the upper border of the fifth dorsal vertebra. The calibre of the left arch is much greater than that of the right arch, and the terminal portion of the left arch lies immediately dorsal to the fistula between the trachea and oesophagus (fig. 3). A small communicating vessel of great interest runs from the posterior aspect of the ascending portion of the right arch to the posterior aspect of the ascending portion of the left arch. The abnormal termination of the abdominal aorta is clearly shown in fig. 4, the inferior mesenteric artery arising as a branch of the single (left) umbilical artery.

Rathke's classical description of the fate of the embryonic aortic arches, as modified by Boas (1887), is shown (fig. 5) for the sake of comparison.

A comparison of fig. 6 with fig. 4 will indicate the nature of the explanation tentatively adduced to elucidate the arrangement of the primitive aortic arches in this foetus. The third arch on each side forms the commencement of the internal carotids. The fourth arch on the right side forms the transverse part of the right systemic arch. The sixth arch on the right persists as far as the outgrowth which forms the right pulmonary artery. The sixth arch on the left persists *in toto* as ductus arteriosus to form the transverse part of the left systemic arch. The small vessel communicating the ascending portions of the two great vessels arising from the heart may be regarded as a persistent fifth left arch, a persistent fourth left arch, or a vessel comparable to the small

artery which is depicted by Tandler ('02), as an "arterien insula" in relation to the aortic arches. The proofs given by Evans ('09) that all the arteries develop originally as well-defined capillary networks permits of a chance



Fig. 5. The aortic arches and their transformations (after Rathke). 1. Ceratodus; 2. Salamander; 3. Triton; 4. Frog; 5. Lizard; 6. Bird; 7. Mammal.

anastomosis persisting along with the definitive arches. Most anatomists would regard this small vessel as a persistent fourth arch because the fifth arch of van Bemmelen (1886) is a transitory structure. Quite as legitimately



one might argue that since the fourth left arch usually persists as the definitive aortic arch, this vessel cannot be the fourth arch. There is no certain means of

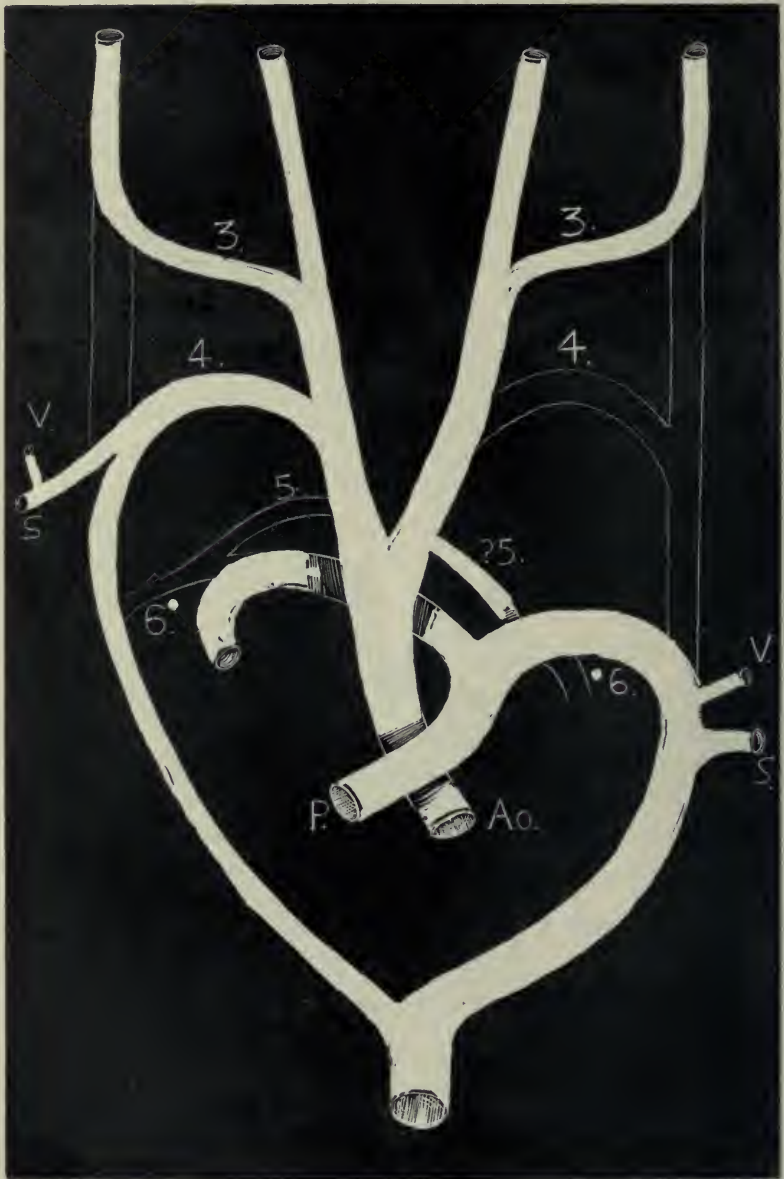


Fig. 6. Transformation of the aortic arches (cf. fig. 4). *Ao.* aorta; *P.* pulmonary; *S.* subclavian; *V.* vertebral; *O* recurrent laryngeal nerves.

ascertaining the identity of this vessel as no trace of the nerve of the fifth arch, the nervus post-tracheicus of the superior laryngeal branch of the vagus (Elze '07) has been recorded in embryos of more than 20 mm.

The work of Bremer ('02, '08) has shown the incorrectness of the conventional diagrams (fig. 5) in which both definitive pulmonary arteries are shown as sharing equally in the proximal parts of the left and right sixth arches, for in no mammal is this true. Man and most of the other mammals have a right pulmonary artery which is of this nature, but the left pulmonary artery is merely the original pulmonary outgrowth of that side, the corresponding proximal portion of its arch having been assimilated in the pulmonary trunk. In this specimen, in accordance with the absence of the left lung there is no trace of the left pulmonary arterial outgrowth from the left sixth arch. The positions of the recurrent laryngeal nerves are shown in fig. 6 and they confirm the tentative explanation of the fate of the aortic arches in this foetus.

The subclavian of the right side is normal and represents the seventh segmental artery with the proximal part of the vertebral as its posterior primary division. The left subclavian artery has not moved cranially so far as the right, so that it retains its attachment to the dorsal aorta in the neighbourhood of the dorsal root of the sixth arch; and the vertebral, by absorption of the proximal part of the seventh segmental artery arises directly from the dorsal root of the sixth arch. This independent origin of the vertebral artery is comparable to the anomalous origin of the vertebral from the arch of the aorta (Thane 1896). Whereas in the latter case the vertebral artery usually enters the foramen transversarium of the fifth cervical instead of the sixth, in this case the vertebral entered the sixth.

The surveys of Tiedemann (1829), Peacock (1866), Turner (1862) and Abbott ('15) provide but few cases in any way comparable to the above, and no identical case has been found in the literature. The cases presenting a resemblance to the one under discussion can be arranged in three groups (Turner 1862):—

1. "Cases presenting atrophy of the fourth left aortic arch between the origins of the common carotid and subclavian arteries, with persistence of the sixth arch."

Greig's (1852) famous case was that of a foetus in which two arteries arose from the base of the heart; one, the aorta, ascended to the right and divided into left common carotid, right common carotid and right subclavian; the other, the pulmonary, gave off a branch to each lung and then continued onwards into the descending aorta which received its supply of blood solely from this source. The left subclavian arose from the latter trunk after it had given off the branches to the two lungs. The ventricular septum was also deficient in its upper part. Breschet reported a case in which the left subclavian arose from the pulmonary artery, but no account is given of the condition of the aorta.

2. "Cases presenting atrophy of the fourth left aortic arch beyond the origin of the subclavian."

This group includes those cases of coarctation of the aorta which are divided into two sub-groups:—

(a) A diffuse narrowing of the aorta at the isthmus [Bonnet's ('03) infantile type]. In some of these cases in which the stenosis is marked, the circulation in the lower part of the body is maintained by a large patent ductus arteriosus



Fig. 7. Aortic system of His' embryo Si. 12.5 mm. *Ao.* aorta; *C.C.* common carotid; *V.* vertebral artery; *P.* pulmonary trunk; *R.P.* and *L.P.* right and left pulmonary arteries.

through which the descending aorta appears to be a direct continuation of the pulmonary artery.

(b) A more or less abrupt constriction of the aorta at or near the insertion of the ductus arteriosus (Bonnet's adult type). Here, where coarction is marked, and has lasted some time, the establishment of an extensive collateral circulation



lends distinctive features to the case. Amongst 212 cases collected by Peacock, Bonnet and Abbott, fifteen cases were of a marked infantile type so that the descending aorta was supplied by a large patent ductus arteriosus. The first case of complete coarctation was that reported by Steidele (1826).

3. "Cases presenting transference of the left subclavian at its origin from the fourth to the sixth aortic arch."

In the case recorded by Holst (1836) the vertebral was given off at the place of junction. A closely similar case was reported by Hildebrand (1842), but the left vertebral arose from the left common carotid.

Thus this particular case is unique in the combination which it presents of a persistent right systemic arch, patent ductus arteriosus with marked coarctation of the fourth left arch, and a small communicating vessel of unknown origin. Still further is it complicated by the absence of the left pulmonary artery.

The 12.5 mm. embryo described by His (fig. 7) presents a right arch of small calibre, a fourth left arch of large calibre and a patent ductus. The obliteration of the fourth left arch and of that portion of the dorsal aorta between the dorsal roots of the fourth and sixth arches on this side would give rise to a condition closely resembling that in the foetus described. Moreover, the relative calibre of the right and left systemic arches in this embryo is approximately the same as in the foetus.

#### D. ABDOMEN AND PELVIS

The anterior abdominal wall is poorly developed. The umbilical vein is normal but the single umbilical artery is disposed to the left, there being no trace of the right umbilical artery to the right of the empty bladder. The viscera are normal in disposition, but the inferior mesenteric artery arises from the left umbilical artery below the bifurcation of the aorta which occurs at the level of the third lumbar vertebra (fig. 4).

The rectum (fig. 8), distended with meconium, reaches to within 1.5 mm. of the surface in the region of the imperforate anus. The viscus presents a well-marked ampulla of 6 mm. diameter which ends by a small canal of less than 1 mm. diameter in a cul-de-sac. There is no fistulous communication between the rectum and the urethra. The main valve of Houston is well-developed at the level of the recto-vesical fold of peritoneum.

The statistics of atresia ani et recti in its various modifications, as collected by Curling (1876), Spriggs ('12) and Keith ('10), show that the commonest anomaly is imperforate anus with recto-urethral fistula opening in the region of the termination of the prostatic urethra. More than 60 per cent. of Keith's male cases fall into this group whereas only seven cases out of 54 present the condition represented in fig. 8, i.e. atresia ani simplex with the rectum ending blindly at the proctodaeum.

The views of the fate of the embryonic cloaca are still conflicting. The generally-accepted view of the division of the cloaca, by downgrowth of a

uro-rectal septum into a ventral urogenital and a dorsal rectal portion, is strongly opposed by the comparative and embryological evidence brought forward by Wood-Jones ('04), who maintains that the cloaca forms the urogenital sinus only, the rectum being developed as a new outgrowth (post-allantoic gut) from the primitive hind gut. Recent work by Pohlman ('11), Buchanan and Frazer ('18) support the former view, and such a view is apparently sufficient to explain the case represented in fig. 8. But this view fails to explain the commonest condition—that in which recto-urethral fistula accompanies imperforate anus. Retterer (1890) describes the separation of the cloaca by two lateral cloacal folds which grow medially and fuse. Zucker-



Fig. 8. Imperforate anus. B. bladder; U. ureter; P.R. prostate; P. peritoneal cavity; R. rectum; V. main valve of Houston.

kandl ('03) states that the division of the cloaca is accomplished by three folds, a median (uro-rectal) and two lateral, which eventually obliterate the tri-radiate space between their free borders. Either of these two views, by supposing incomplete fusion of the septa, will explain the persistence of a communication between the two derivatives of the cloaca. Such a view would necessitate a wide degree of variation in the position of the fistulous communication.

According to Wood-Jones, the recto-urethral fistula is a persistence of the cloacal anus of the early embryo—comparable to the cloacal anus of *Echidna*. This cloacal anus which is doomed to be exchanged for the definitive anus of the adult is bounded cranially by that sheet of recto-cloacal muscle which

can be recognised in every adult pelvis as the recto-urethral muscle, and marks the most caudal limit of the peritoneal cavity in the recto-vesical pouch, which is of great depth in the foetus. In the adult, the recto-urethralis muscle consists of longitudinal fibres of the rectum which sweep downwards and forwards to the apex of the prostate and reascend in the muscular coat of the prostatic urethra (Elliot Smith '08). The main rectal valve of Houston (fig. 8) serves to demarcate the site of this early embryonic communication.

Thus this case of atresia ani serves to illustrate the need for a comprehensive examination of the development of the hind-end of the body.

The testicles are situated at the internal abdominal rings and their progress through the abdominal wall has commenced, as is shown by the extension of the gubernacula along the inguinal canals. The right kidney, suprarenal and ureter are normal, but there is no trace of the left kidney, left ureter or left renal vessels. The left suprarenal is present. Both suprarenals and the right kidney are free from any abnormality of size and position, though the left suprarenal exhibits some alteration in shape owing to the absence of the left kidney. The trigonum of the bladder presents a patent right ureteric orifice but there is no trace of the left. The urethra and prostate are normal.

The absence of one kidney is a matter of interest to the surgeon and its occurrence is as frequent as that of imperforate anus, roughly one in 5000. Previous to the masterly analysis of Sir Henry Morris, the observers failed to differentiate clearly between entire absence of one kidney, congenital atrophy of one kidney and fusion of two kidneys. The statistics of Thompson ('13) and Gladstone ('14) show that the left kidney is absent about twice as often as the right, and that deformities of the urogenital organs are not the only congenital defects which may accompany the condition. The corresponding suprarenal is present in 90 per cent. of the cases in which one kidney is absent.

The right kidney in this case is normal in size, position, and blood supply, definitely disproving the statement frequently reiterated that a single kidney always exceeds the normal in size (Craven Moore, Gladstone). As Morris says, "an unsymmetrical kidney, like a renal mass composed of two kidneys fused together, may be either of much greater magnitude than the normal kidney, or not at all in excess of the normal." The question of hyperplasia versus hypertrophy of the glomerular elements has been discussed by Galeotti and Santa ('02), Eckardt (1888), Moore ('06) and Boycott ('10-'14).

The Wolffian duct reaches the cloaca in the 4 mm. embryo (Mall) and presents no traces of the renal bud. The renal bud appears near the termination of the Wolffian duct in the 5 mm. embryo. Thus the upgrowth of the renal bud to form the ureter and kidney occurs between the 4.5 and 5 mm. stage and proceeds so rapidly that the hilum of the kidney reaches its adult position by the end of the second month. Suppression of one kidney appears to be due to failure of the outgrowth from the hind end of the Wolffian duct, with the



result that the ureteric orifice is absent although the testis, vas, and ejaculatory ducts may be normal. Gladstone says that "congenital absence of the kidney and ureter is in all probability due to an arrest in the development of the distal end of the Wolffian duct and to a failure in its union with the cloaca." This explanation will not account for the presence of a normal testis and vas deferens in this case.

As Felix ('12) has shown there is no close parallel between the segmentation of the mesonephros and the somatic segments; the condition is one of marked dysmetamerism. In the 2.5 mm. embryo the mesonephros extends from the second to the fourth thoracic segments with eight well-developed tubules. In the 4.25 mm. embryo the mesonephros extends from the seventh cervical to the second lumbar segment and contains 28 tubules. Thus the mesonephros grows both caudally and cranially. The cranial growth is completed in an

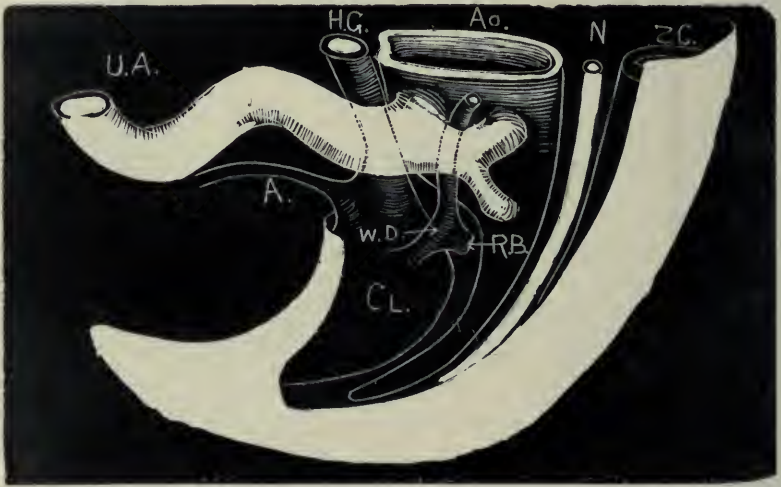


Fig. 9. Reconstruction of the arteria umbilicalis in a human embryo 5.3 mm. long. The umbilical artery is seen to arise from the aorta by three roots, a visceral and two parietal (after Felix, 1910). *Ao.* aorta; *U.A.* umbilical artery; *H.G.* hind gut; *CL.* cloaca; *A.* allantois; *W.D.* Wolffian duct; *R.B.* renal bud; *N.* notochord; *S.C.* spinal cord.

embryo of 5.3 mm. (at the fifth cervical) and the caudal growth in an embryo of 7 mm. (at the third lumbar). Immediately the cranial growth is completed, degeneration sets in at the cranial end, so that ultimately the mesonephros is limited to the lumbar segments.

The ureteric bud appears at first between the 4.5 mm. and 5.3 mm. stage on the dorsal wall of the Wolffian duct and then inclines more and more towards its medial surface (Felix '12). This secondary medial position is of importance from the comparative point of view, since it persists throughout life in the marsupials and in these forms is an obstacle to the union of the two Müllerian ducts (Keibel 1896). At this stage (fig. 9) the Wolffian duct lies between the visceral (primary) and parietal (secondary) roots of the

umbilical artery. Persistence of the visceral root will offer a serious hindrance to the development of the ureteric bud for, as is well shown by the clinical history of arterial aneurism, every tissue has to give way to an expanding artery. Therefore it is suggested that persistence of the primary visceral root of the umbilical artery may prevent the development of the renal bud. This still leaves one faced with the difficulty of accounting for the persistence or late disappearance of this visceral root.

In the 1·38 mm. embryo (Kroemer-Pfannenstiel) the umbilical artery arises by several roots in common with the vitelline arteries at the level of the fourth cervical segment, and migrates caudally to reach the fourth lumbar segment at the 5·3 mm. stage when both visceral (primary) and parietal (secondary) roots exist for a short time coincidently, so as to form an arterial ring enclosing the Wolffian duct (Keibel and Elze '08). Thus, during their caudal migration, the umbilical arteries must have passed over those segments, eighth and ninth thoracic, which show complete suppression on the left side, as displayed by the absence of the two half vertebrae, eighth and ninth ribs, and eighth and ninth thoracic nerves. One is tempted to suggest that this foetus, somewhere near the 4·5 mm. stage, was subjected to an arrest in development in the precartilaginous stage which led to defective development of the heart, great vessels and lungs, defective development of the left half of the eighth and ninth thoracic segments, defective development of the left kidney, and defective development of the cloacal membrane. The obvious objection to the above is the disposition of the vascular, lung, renal and upper limb anomalies to the left side of the body, whereas the umbilical artery is defective on the right side. The primitive defect of segmentation may be closely associated with an exaggeration of that degree of asymmetry of the embryonic axis which von Baer described almost a hundred years ago as a normal characteristic of the embryo.

My thanks are due to Mr Bendit, of University College Hospital, who procured the specimen: to my colleagues in the Anatomy, Radiographic and Gynaecological Departments who have been my ready helpers; and to Mr Gerrard, of the Slade School of Art, who has devoted much labour to the preparation of the wood-cuts.

#### ADDENDUM

Opportunity has recently been afforded for the examination of a full-term male baby aged three weeks of the same parentage. The baby presents buphthalmia, bilaterally symmetrical naevi of the naso-facial angle and hypospadias. This confirms the ancient dictum that the mother who gives birth to a merosomatous monster is more likely to give birth to another merosomatous monster than to a normal child.

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## REVIEW

*A Laboratory Manual for Comparative Vertebrate Anatomy.* By LIBBIE H. HYMAN. The University of Chicago Press. Chicago, Ill.

There may be conflicting views concerning the method of inculcating the facts of comparative vertebrate anatomy but there can be little doubt that Dr Hyman has rendered a service to practical zoology the world over in the publication of this book which represents the outcome of a successful and efficient working of the "system by system" plan over several years in a large university.

This "comparative" method, although commended from the theoretical point of view, is generally scouted as unworkable on the grounds of its prodigal demands in material. The experience at Chicago has exposed the falsity of the contention. It now remains to be seen whether this local success will affect the general teaching of zoology in America and in the British Empire. A firmly-grounded trust in the well-tried "type" method and a staunch adherence to tradition are the factors which are likely to militate against the widespread use of the text-book in this country.

The treatment is generally well-balanced, its tone illustrating admirably the intensity of the American scholastic method. One feels however that a sensitive spirit will recoil at finding such statements as "the liver *is compelled to grow into the septum*" or "The two pleural cavities.....*split* the pericardium from the ventral body wall." An earnest effort is made to render clear the ever-elusive body cavities and the circulatory system is enriched by the recent publications of Huntington and McClure, but the central nervous system is presented as inadequately as in the majority of zoological text-books and the word "visceral" has worked its usual havoc in the nervous, skeletal and muscular systems. When shall we hail the day of its disappearance along with the three specific germ layers, the endodermal origin of the segmented mesoderm, the ectodermal origin of neuroblastic tissue, the archenteric coeloma—all that dogmatic crew which have hitherto manned the zoological ship of state?

The pictures are schemata for the most part, but there is design in this treatment, the student being expected to make drawings from his own preparations—a practice greatly to be commended. Whether he should be relieved of making his own summaries is another matter.

In providing a suitable glossary, important direct practical hints and an ample index, the author has afforded addenda which are frequently overlooked in texts of this nature. Here is a worthy addition both to the student's bookshelf and to the teaching of comparative anatomy.

R. A. D.

# ON THE LARVAL HYOBRANCHIAL SKELETON AND MUSCULATURE OF *CRYPTOBRANCHUS*, *MENOPOMA*, AND *ELLIPSOGLOSSA*

BY F. H. EDGEWORTH, M.D.

THE hyobranchial skeleton of the adult stages of these Amphibia is now well known. That of *Cryptobranchus japonicus* s. *Sieboldia maxima* s. *Megalobatrachus maximus* has been described by Schmidt, Goddard, and van der Hoeven (1862), Fischer (1864), Hyrtl (1865), Parker (1882), Osawa (1902), and Drüner (1904). That of *Menopoma alleghaniense* s. *Cryptobranchus alleghaniensis* was described by Stannius (1856), Fischer (1864), Hyrtl (1865), Wiedersheim (1877), Parker (1882), Wilder (1892), and Drüner (1904). That of *Ellipsoglossa naevia* and *nebulosa* s. *Hynobius naevius* and *nebulosus* was described by Wiedersheim (1877) and Drüner (1904). An admirable critical summary of these observations was given by Gaupp in 1904.

On the other hand the larval conditions, except for some observations on the development of the urobranchiale in *Menopoma* and *Ellipsoglossa*, which I published in 1920, have not yet been described.

The following pages contain descriptions of the hyobranchial skeleton of the larvae of these Urodela. Gaupp's nomenclature has been followed. The figures have been drawn from models made by the wax-plate method. Each description is followed by a discussion of the changes which take place between the larval and adult conditions. To facilitate this, outline drawings of the adult state, taken from papers published by the above mentioned authors, have been introduced. This is followed by a short account of the muscles attached to these larval structures and by a discussion of the differences between the larval and adult conditions. Drüner's masterly account has been taken as the basis of these comparisons.

In a 37 mm. larva of *Cryptobranchus japonicus* the hyobranchial skeleton consists of a median basibranchiale<sup>1</sup> and the extremity of the urobranchiale, and on each side of the hyoid and four branchial bars. The hyoid bar consists of keratohyal and hypohyal

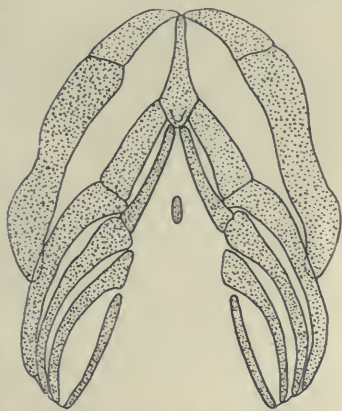


Fig. 1. *Cryptobranchus japonicus* larva, 37 mm.

<sup>1</sup> By "basibranchiale" I mean the rod extending from the hyoid to the 2nd branchial bars. Theoretically it consists of basibranchiale i + basibranchiale ii, but it is a continuous structure and is formed as such—not in two separate pieces.



elements separated by a joint, the 1st branchial bar of keratobranchial and hypobranchial elements separated by a joint, the 2nd similarly, whilst the 3rd and 4th consist solely of keratobranchialia. The upper ends of the keratobranchialia are tied together by ligaments. The ventral end of keratobranchiale iii is attached to keratobranchiale ii by a cellular tissue, and keratobranchiale iv to keratobranchiale iii similarly. On the medial side of the ventral end of keratobranchiale i is a process which articulates with hypobranchiale i. The adjacent dorsal end of hypobranchiale i does not take part in the joint.

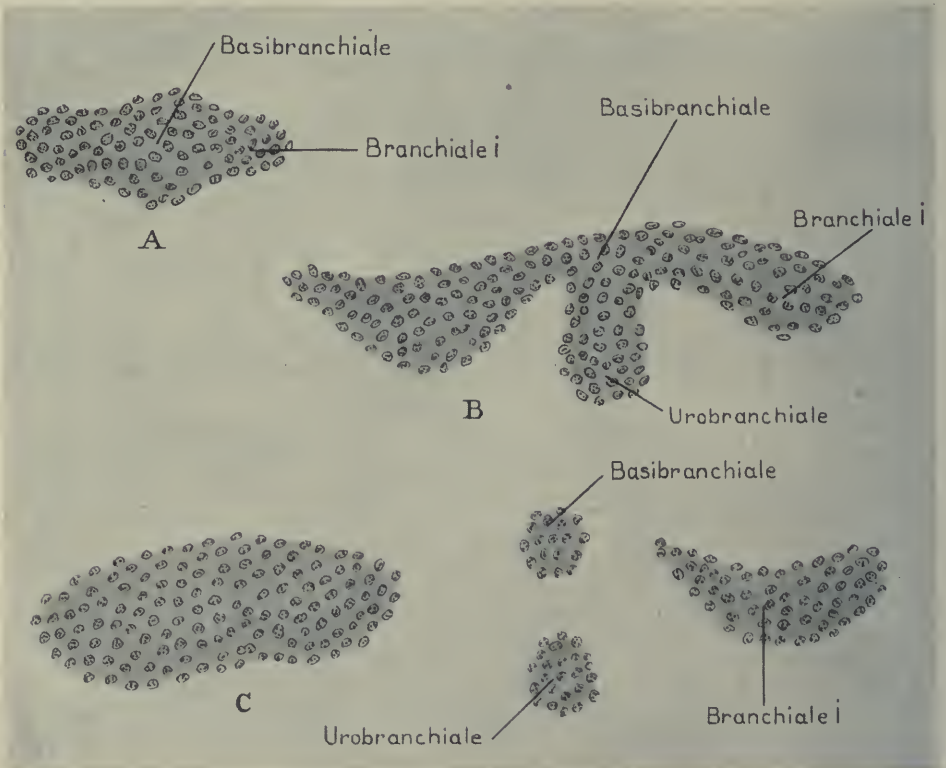


Fig. 2. *Cryptobranchus japonicus* larva, 15 mm. Transverse sections showing the urobranchiale. A is the most anterior section.

The basibranchiale is a median rod, slightly broader posteriorly than anteriorly. The ventral ends of the hypohyalia and the anterior end of the basibranchiale meet in a  $\Lambda$ -shaped joint. Hypobranchiale i articulates with the side of the basibranchiale and hypobranchiale ii with its hind end. There is a slight ventral projection of the posterior part of the basibranchiale, which is the stump of the urobranchiale. The distal end of the urobranchiale persists as a separated nodule of cartilage, whilst the main portion has disappeared. All the joints are syndesmotie in character.

In a 15 mm. larva of *Cryptobranchus japonicus* (fig. 2) the hyobranchial skeleton forms a slightly chondrified continuous structure, without any joints. The anterior end of the basibranchiale forks and joins the ventral ends of the hyoid bars. The 1st branchial bar is continuous with its side and the 2nd with its hind end. The urobranchiale is a ventro-posterior outgrowth of the basibranchiale just behind the junction of the 1st branchial bars. The ventral ends of these bars extend downwards a little along the proximal part of the urobranchiale.

The urobranchiale is thus an outgrowth of the 2nd basibranchial constituent of the basibranchiale, just as in *Menopoma* and *Ellipsoglossa*, and, as in the latter, there is a ventral extension of the 1st branchial bars along it.

The changes which occur in the hyobranchial skeleton between the larval and adult states (figs. 3, 4, 5) are: (1) The joint between the keratohyale and hypohyale generally persists; in Fischer's specimen it had disappeared. (2) In



Fig. 3. *Cryptobranchus japonicus* adult (Schmidt, Goddard and van der Hoeven.)



Fig. 4. *Cryptobranchus japonicus* adult (Hyrtl).

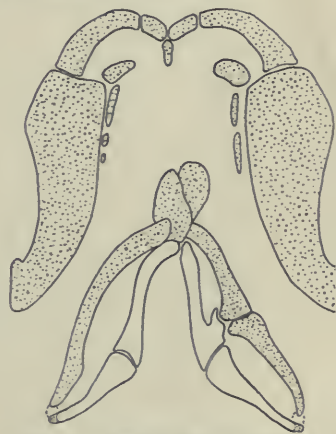


Fig. 5. *Cryptobranchus japonicus* adult (Drüner).

one specimen Drüner found three cartilages—a median and two lateral—in the ventral part of the hyoid bars. He regarded all three as parts of a copula. The articulation, however, of the anterior end of the basibranchiale with the ventral ends of the hypohyalia in the larva suggests that the lateral cartilages of the adult are separated parts of the hypohyalia. (3) Small nodules of cartilage are separated from, or are formed close to, the kerato- and hypohyale. (4) The joints between the dorsal and ventral elements of the 1st and 2nd branchial bars may persist or disappear. (5) The joint between keratobranchiale i and hypobranchiale ii exceptionally persists—for Drüner found on one side of one adult specimen a joint between the adjacent ends of kerato- and hypobranchiale i and hypobranchiale ii. (6) Ossification occurs in the kerato- and hypobranchial elements of the 2nd branchial bar. (7) Keratobranchialia iii and iv disappear. (8) The anterior end of the basibranchiale either fuses with the ventral ends of the hypohyalia (Schmidt, Goddard and van der Hoeven,

Fischer, Parker, Osawa, Drüner), or remains as an isolated nodule of cartilage just behind the united ends of the hypohyalia (Hyrtl, Drüner). The next succeeding portion of the basibranchiale disappears. Its posterior part enlarges to a plate, with which articulate the ventral ends of the 1st and 2nd branchial bars. In one specimen (Hyrtl) its posterior end was segmented off. (9) Atrophy of the urobranchiale begins, and is probably completed, during larval life.

In a 40 mm. specimen of the larva of *Menopoma* (fig. 6) the hyobranchial skeleton consists of a basibranchial, and on each side of a hyoid and four branchial bars. The hyoid bar consists of kerato- and hypohyal elements, separated by a joint. The ventral ends of the hypohyalia articulate with each other, and with the anterior end of the basibranchiale, by a  $\Lambda$ -shaped joint. The first branchial consists of kerato- and hypobranchial elements separated by a joint. There is a median projection of the lower end of keratobranchiale i, but it is only connected to hypobranchiale ii by loose connective tissue, and there is no definite joint as in *Cryptobranchus*. The lower end of hypobranchiale i articulates with the side of the basibranchiale. The second branchial bar consists of kerato- and hypobranchial elements, separated by a joint. The ventral end of the latter articulates with the posterior end of the basibranchiale. The third branchial bar consists of kerato- and hypobranchial elements. The latter is rather long, and its lower end lies median to the upper end of hypobranchiale ii. The fourth branchial bar consists solely of a keratobranchial element. The basibranchiale is a straight median rod, rather narrower anteriorly than it is further back. There is no urobranchiale—this having, as previously described, atrophied by this stage.

The changes which occur between the larval condition and the adult stage (figs. 7–10) are as follows: (1) Partial ossification of the keratohyale, the keratobranchialia, and hypobranchiale ii; that of keratobranchialia is variable. (2) Various small cartilages are segmented off, or developed close to, the kerato- and hypohyale. (3) Two conditions have been found in the ventral part of the hyoid bar; either a single cartilage (Fischer)—the hypohyale, or two cartilages—a dorsal and a ventral (Hyrtl, Wiedersheim, Parker, Wilder, Drüner). Hyrtl and Wiedersheim were of opinion that the two ventral cartilages represent a basihyale; Wilder, that they represent the anterior copula of Fischer; Drüner, that they represent a paired copula. The two latter did not express any opinion of the nature of this copula—whether a basihyale or a basibranchiale. On the other hand Parker thought that they represent portions of the hypohyalia. The first theory may be rejected, as no basihyale—no median cartilage in front of the hyoid bars—is present in larval life. Further, the articulation of the anterior end of the basibranchiale with the ventral end of the hypohyalia in the larva supports Parker's theory. It may be concluded that the hypohyale generally separates into an upper and a lower piece. (4) The persisting anterior end of the basibranchiale may be situated between the hypohyalia (Fischer), or just behind them (Parker, Drüner), or be absent (Wilder). The next succeeding



portion of the basibranchiale atrophies, whilst the posterior part enlarges to a plate<sup>1</sup>, with which articulate the 1st and 2nd branchial bars. In Parker's specimen the hinder end of this plate was segmented off. (5) In two adult specimens of Drüner's there was a hypobranchiale iv, which was probably a feature persisting from larval life. It was not present in the larva depicted.

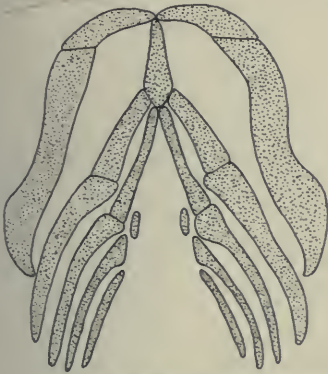


Fig. 6. *Menopoma* larva, 40 mm.

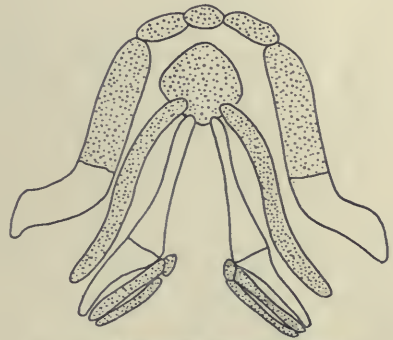


Fig. 7. *Menopoma* adult (Fischer).

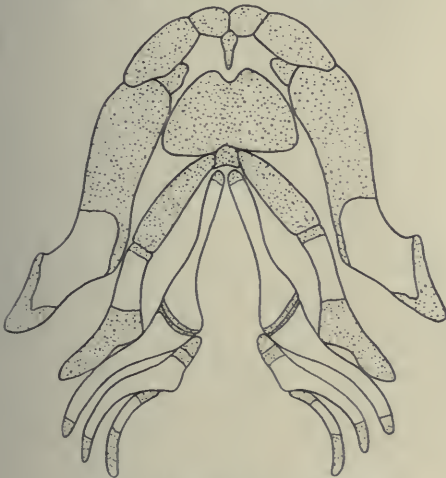


Fig. 8. *Menopoma* adult (Parker).

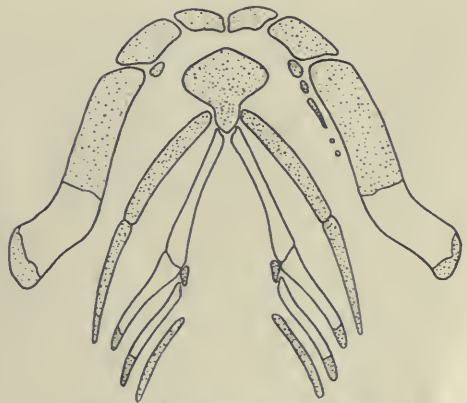


Fig. 9. *Menopoma* adult (Wilder).

In a 30 mm. larva of *Ellipsoglossa nebulosa* (fig. 11 and 12) the hyobranchial skeleton consists of a median basibranchiale and urobranchiale, and on each side of a hyoid and four branchial bars. Each hyoid bar consists of keratohyal and hypohyal elements, the first three branchial bars of keratobranchial and hypobranchial elements, and the 4th branchial bars solely of a

<sup>1</sup> I might mention that in a larva of 34 mm., i.e. one presumably younger than the 40 mm. specimen from which the model was constructed, and certainly possessing the cartilaginous distal end of the urobranchiale, the basibranchiale had undergone enlargement to a plate in front of the articulation of the 1st branchial bars. This appears to have been a premature development of the adult condition.

keratobranchiale. Hypobranchiale iii is a small nodule of cartilage at the ventral end of keratobranchiale iii. The basibranchiale is a straight median rod the anterior end of which articulates with the hypophyalia. The ventral ends of hypobranchialia i are continuous with the basibranchiale and the proximal end of the urobranchiale, and extend a little down the latter. Hypobranchialia ii articulate with the hind end of the basibranchiale. The ventral end of keratobranchiale iii



Fig. 10. *Menopoma* adult (Drüner)

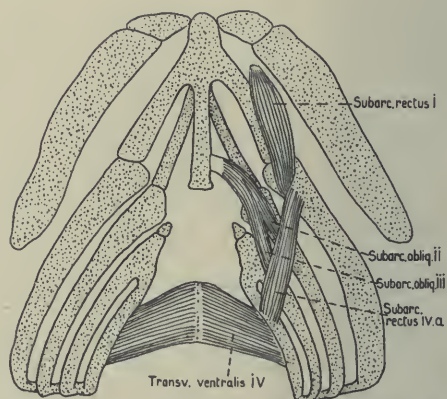


Fig. 11. *Hynobius nebulosus* s. *Ellipsoglossa nebulosa* larva, 30 mm. Ventral aspect.

and the hypobranchiale iii are tied to keratobranchiale ii by a cellular tissue. The ventral end of keratobranchiale iv is continuous with keratobranchiale iii. The dorsal ends of the keratobranchialia are continuous. The joints between the dorsal and ventral elements of the hyoid and first two branchial bars, and between the basibranchiale and the hypophyalia and hypobranchialia ii are syndesmotic in character.

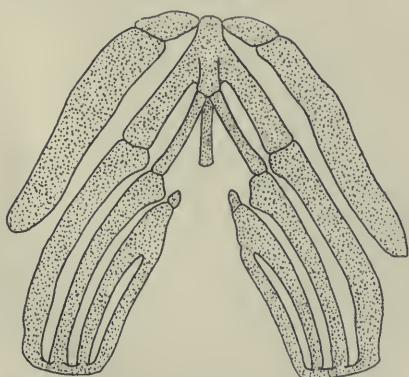


Fig. 12. *Hynobius nebulosus* s. *Ellipsoglossa nebulosa* larva, 30 mm. Dorsal aspect.

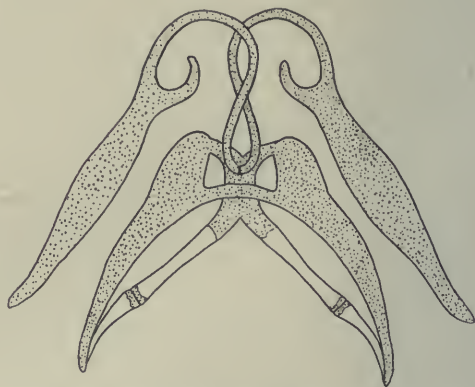


Fig. 13. *Hynobius naevius* s. *Ellipsoglossa naevia* adult (Wiedersheim).

The changes which occur between this condition and the adult state (fig. 13) are: (1) The hypophyalia probably develop into the long cartilaginous filaments

which turn backwards and are connected together by connective tissue. (2) A curved process develops from the ventral end of the keratohyale. Gaupp suggested that it is homologous with the cartilaginous nodule developing in a similar position in *Cryptobranchus* and *Menopoma*. (3) Kerato- and hypobranchiale i fuse, forming a continuous rod. (4) Ossification occurs in kerato- and hypobranchiale ii. The ventral end of the latter becomes continuous with the hind end of the basibranchiale. (5) Keratobranchialia iii and iv disappear. (6) The anterior portion of the basibranchiale disappears. The downward prolongations of the ventral ends of hypobranchialia i along the urobranchiale persist as a transverse bar connecting the 1st branchial bars ventral to the basibranchiale. (7) The urobranchiale disappears. In one specimen of Drüner's its posterior end persisted.

#### ON THE MUSCLES CONNECTED WITH THE HYOBRANCHIAL SKELETON.

A description of the ventral hyobranchial muscles of the larvae of *Menopoma* and *Ellipsoglossa* has already been given. Subarcualis rectus i, subarcuales obliqui ii and iii, subarcualis rectus iv *a* and transversus ventralis iv, are represented in the model of *Ellipsoglossa*. Subarcualis rectus iv *b* and *c* are minute fasciculi on the dorsal side of subarcualis rectus iv *a*, and are not represented.

Those of the larva of *Cryptobranchus* are very similar—subarcualis rectus i arises from keratobranchiale i and is inserted into the median side of the ventral end of the 2nd gill-cleft (not having yet gained an insertion into the hyoid bar). Subarcuales obliqui ii and iii arise from keratobranchiale ii and iii, pass inwards and downwards, unite, and are inserted partly into the distal end of the urobranchiale and partly into the fascia of the rectus cervicis profundus. Subarcualis rectus iv arises from keratobranchiale iv, and separates into *c*, *b*, and *a*, which are inserted into keratobranchialia iii, ii, and i, respectively. The genio-hyoideus is inserted into the posterior end of the urobranchiale, fascia of the rectus cervicis profundus and hypobranchiale ii. It is not so distinctly separated into medial and lateral fasciculi as in *Menopoma*. The rectus superficialis is inserted into the urobranchiale, the rectus profundus into the basibranchiale and hypobranchialia i and ii. Transversus ventralis iv partly underlies the pharynx, partly the larynx. The laryngeal muscles consist of dilatator laryngis, laryngei, and constrictor laryngis. As regards other muscles. The keratohyoideus externus exists in all three larvae, arising from the dorsal end of keratobranchiale i and passing down outside the hyoid bar. In *Cryptobranchus* and *Menopoma* it is inserted to the lower end of the keratohyale, in *Ellipsoglossa* it extends to the hypohyale. It is interesting to observe that Drüner—who had only adult specimens at his disposal—inferred the existence of this muscle in the larvae from the presence of fine branches of the r. jugularis vii ending in connective tissue in front of the anterior end of subarcualis rectus i. The interhyoideus has spread backwards in the opercular fold, but is not separated into the interhyoideus



and constrictor colli of the adult. It is attached dorsally to the keratohyale and keratobranchiale i. All four levatores arcuum branchialium are present. The first arises from the auditory capsule above the origin of the depressor mandibulae, the others from the dorsal fascia. Levator iv is succeeded by dorso-pharyngeus iv and this by the trapezius. In *Ellipsoglossa*, but not in *Cryptobranchus* or *Menopoma*, an omo-arcualis is present—arising from the dorsal end of keratobranchiale iv, and passing back to the shoulder girdle. Gill-muscles are present—the levatores branchiarum arise from keratobranchialia ii and iii. The transversus ventralis iv underlies the pharynx and larynx.

The changes in the hyobranchial musculature which take place between the larval and adult stages of *Cryptobranchus* are: (1) The interhyoideus separates into the interhyoideus and constrictor colli. The former gains an additional origin from the quadrate; the origin of the latter losing its attachment to keratobranchiale i grows up to the dorsal fascia. (2) The ceratohyoideus atrophies. (3) The gill-muscles atrophy. (4) Subarcualis rectus i gains an insertion to the kerato- and hypohyale. (5) The dorso-pectoralis is developed—probably from the trapezius. (6) In association with the loss of the 3rd and 4th branchial bars, the broadening of the posterior part of the basibranchiale, and the atrophy of the urobranchiale, the following changes take place: (a) Levatores arcuum branchialium ii and iv and the dorso-pharyngeus iv join with transversus ventralis iv to form a muscle-complex—the dorso-pharyngeus; in which there is a lateral inscription, the ligamentum branchio-pectorale. (b) The origin of subarcualis obliquus ii shifts to either the lig. branchio-pectorale or to the keratobranchiale ii. (c) Subarcualis rectus iv atrophies. (d) The subarcuales obliqui, the rectus superficialis, and the medial fibres of the genio-hyoideus are inserted to an inscription between the two latter muscles. (e) The rectus profundus loses its insertion to hypobranchialia i and ii. (7) The ventral portion of the dorso-pharyngeus, i.e. the original transversus ventralis iv, underlies the trachea. This is probably due to a forward shifting of the larynx.

Very few changes occur in the hyobranchial musculature of *Menopoma* between the larval and adult stages. (1) The ceratohyoideus externus atrophies. (2) The interhyoideus separates into the interhyoideus and constrictor colli. The former gains an additional origin from the quadrate; the latter loses its origin from keratobranchiale i and gains one from the dorsal fascia. (3) Subarcualis rectus i gains an insertion to the kerato- and hypohyale. (4) Levator arcuum branchialis i atrophies. (5) The medial part of the genio-hyoideus, the rectus superficialis and the obliqui become inserted to an inscription between the two former. (6) Transversus ventralis iv lies under the trachea, probably owing to a relative forward shifting of the larynx.

In *Ellipsoglossa* the following changes occur between the larval and adult stages. (1) The interhyoideus of the larva separates into the interhyoideus and constrictor colli of the adult. The former separates into the subhyoideus

and the m. inter ossa quadrata. The latter loses its attachment to keratobranchiale i and becomes more longitudinal in direction. (2) Levator arcus branchialis i atrophies. (3) Ceratohyoideus externus atrophies. (4) The gill-muscles atrophy. (5) Subarcualis rectus i gains an insertion to the keratohyale. (6) The following changes occur in relation to the loss of the 3rd and 4th branchial bars and of the urobranchiale: (a) Levatores iii and iv and dorso-pharyngeus iv together with transversus ventralis iv forms the dorso-pharyngeus. (b) Subarcualis rectus iv atrophies. (c) Subarcualis obliquus iii gains an origin from the inscriptio in the dorso-pharyngeus, and it and subarcualis obliquus ii become inserted into the fascia of the rectus superficialis. (d) The genio-hyoideus becomes continuous with the rectus superficialis. (e) The origin of the omo-arcualis from keratobranchiale iv is lost and one is gained from the inscriptio in the cephalo-dorso-pharyngeus (= omo-pharyngeus of Drüner). (7) A very slight shifting forward of the larynx relative to the transversus ventralis iv occurs.

I owe many thanks to Prof. Hill for three larvae of *Cryptobranchus japonicus*, to Prof. Watasé for his help in obtaining a fine series of larvae of *Ellipsoglossa*, and to Mr J. F. G. Wheeler for the macroscopic drawings. I should also like to acknowledge the efficient assistance of Mr Emery, laboratory attendant.

The expenses incurred in obtaining the larvae, of the investigation, and of the illustrations have been paid by the Colston Research Society.

April 20, 1922.

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# FACTORS BEARING UPON THE ETIOLOGY OF FEMORAL HERNIA<sup>1</sup>

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## INTRODUCTION

THE student who, in his anatomy days, is dissecting the femoral region for the first time, is surprised, and usually mystified, by a long and elaborate description of the course taken, and relations presented, by a femoral hernia in its passage from the abdomen into the leg. An unoccupied interval is described to him, between the femoral vein and the free edge of Gimbernat's ligament. This is bounded by Poupart's ligament in front and by bone behind. He is informed that, through this quadrilateral "ring" which constitutes the upper orifice of a so-called "canal" (the crural canal) along the innermost compartment of the femoral sheath, almost any abdominal content may, under certain circumstances, reach the thigh.

Two facts are, as a rule, very clearly put forward for his notice. These are as follows:

(1) Femoral hernia is commoner in females than in males.

(2) This is because the crural ring is wider in the female. The basis for the second point, which may be either stated or inferred by the books, is that the female pelvis is wider than the male, and hence it is assumed, the female crural ring *must* be wider.

Cunningham's *Practical Manual of Anatomy* (1910 edition), in speaking of femoral hernia, states:

Here then is a weak point in the parietes of the abdomen, and one, which is greater in the female than in the male, seeing that in the former the distance between the pubic and iliac spines is proportionately greater, and in consequence the crural ring wider. Femoral hernia, therefore, is more common in the female.

At any rate, whether it be statement or inference, the conception of a wider pelvis being responsible for the greater frequency of this type of hernia in women, is apt to remain permanently in the student's mind, and not only that, but also in most cases to represent to him the end of the whole matter. When he comes to surgery the same thought is usually fostered.

The following are extracts from two well-known surgical text-books:

(1) Femoral hernia occurs most commonly in women, on account of the

<sup>1</sup> This thesis was submitted for the degree of M.D. at Manchester in May 1921 and was awarded a gold medal.



greater expansion of the iliac crests allowing increased space beneath Poupart's ligament, and especially in those who have borne children.

Rose and Carless, *Surgery*, 10th ed. 1920.

(2) Femoral hernia is oftenest met with in the female, probably because the pelvis is wider, the femoral ring is larger, and Gimbernat's ligament less strongly developed, in women than in men, and it is most common in women who have borne children.

Thomson and Miles, *Manual of Surgery*, vol. II. 1915.

Such statements as these are calculated to convey a similar impression.

It is on account of frequent observations of statements similar to those cited, that this investigation has been undertaken. It has always seemed to me, that to lay the whole responsibility of a greater incidence of femoral hernia in women, upon the fact of a wider pelvis, is an easy, doubtful and unsatisfactory way of shelving the difficulty.

The enquiry undertaken in the work which has been done, has been largely directed towards an investigation of the truth or untruth of this widely-disseminated statement. The scope, however, has been wider than this. Many other anatomical points have been considered, in a comparison of the femoral regions of the two sexes.

Although a desire to investigate this subject, chiefly with the object of discovering what factors are mainly concerned in producing femoral hernia more frequently in one sex than in the other, originally impelled me to take up the task, the causation of this type of hernia, apart from sex, has not been omitted.

#### SOURCES OF MATERIAL, ACKNOWLEDGEMENTS, ETC.

Professor J. S. B. Stopford has very kindly permitted me to make use of all the specimens and material in the Department of Anatomy of the University of Manchester.

A large number of innominate bones and two of the dissections of "soft parts" for the measurement of ligaments, etc., in the femoral region have been drawn from this source. I desire to express my heartiest thanks to him for his kindness, for much valuable advice, and for the constant interest which he has shown in the work.

All the Egyptian innominate bones which have been measured, belong to the collection of Egyptian remains made by Professor G. Elliot Smith, and presented to the Anatomical Department in the Manchester University. For the use of the material of the Post-Mortem Room at the Manchester Royal Infirmary, I am indebted to Professor H. R. Dean and to Dr W. B. Anderton of the Pathological Department. A large draw has been made upon this source, 54 cases having been examined in the Post-Mortem Room. For facilities given me for the measurement of female pelves in the wards of the Manchester Royal Infirmary, and for the opportunity of collecting records of 100 cases of femoral hernia there operated upon, I have to thank Mr R. L. Newell, late Surgical Registrar of that hospital. For a similar opportunity

of measuring male pelves at the Ancoats Hospital, I am obliged to Dr Critchley and to Dr Gordon Whitehead.

I also desire to express my thanks to Dr Fothergill, Mr Ray, and Mr Geoffrey Jefferson for the loan of a pelvimeter, facilities to measure patients, and for valuable suggestions, respectively.

All the photographs and microphotographs used in the illustration of the text were taken for me by Mr Gooding, Histologist to the Anatomical Department. I am also obliged to him for the cutting and staining of histological sections of the femoral sheath, and of femoral hernia sacs. Some of the photographs are from specimens: others from sketches prepared by myself, to illustrate points referred to in the text.

### INTRODUCTORY REMARKS

In the following account and investigation of the factors bearing upon the etiology of femoral hernia, it has been deemed convenient to set forth the subject, under the following headings:

*Part I.* The Gross Anatomy of the Femoral Region.

*Part II.* Factors arising out of Comparative Anatomy and Morphology.

*Part III.* Factors arising out of the Anatomy of the Femoral Region.

*Part IV.* Factors arising out of Developmental Processes.

*Part V.* Factors arising out of Physiological and Pathological Processes.

### Part I

#### THE GROSS ANATOMY OF THE FEMORAL REGION

The anatomy of the femoral region embraces in the main an account of all the structures which lie between the superior or abdominal surface of the pubis and ilium on the one hand, and Poupart's ligament on the other, together with an account of these bounding structures. This interval beneath Poupart's ligament, through which the false pelvis communicates with the leg, may be conveniently referred to as the "pelvo-crural space."

*Innominate bone.* If one takes an innominate bone and holds it so that its crural surface is towards the observer, one is easily able to locate the angle of the pubis and the anterior superior iliac spine. From the former point, running transversely outwards for  $1-1\frac{1}{4}$  inches, is a rough border of bone, the pubic crest, terminating in an eminence, well marked and of a somewhat triangular shape—the pubic spine.

Taking this point as our first landmark, it is obvious that *internal* to this the superior aspect of the innominate bone is practically linear (the pubic crest), whereas *external* to it, it presents a surface, ever widening as it is traced outwards towards the anterior superior iliac spine, and eventually passing imperceptibly into the iliac fossa. The posterior border of this surface is the ilio-pectineal line which demarcates the false pelvis (above and in front of it) from the true pelvis (below and behind it). This border commences at the

pubic spine and curves evenly round to end near the upper part of the "auricular surface." The anterior border runs at first almost transversely outwards and then upwards with a marked and varying inclination outwards. The transverse portion begins at the pubic spine and is formed at first of the smooth rounded anterior border of the ascending ramus of the pubis, and then passing over the enlarged outer extremity of this, it is in the second place constituted by the upper part of the iliac portion of the acetabular rim. The vertical portion consists only of the anterior border of the ilium, and presents the anterior superior, and anterior inferior, iliac spines, separated by a notch. The surface which is included between the borders described, is somewhat triangular, and is, in the main, concave. The enlarged outer and acetabular part of the ascending ramus of the pubis, projects upwards however, forming the ilio-pectineal eminence. Although forming a low-lying, and usually fairly smooth boss of bone, this temporarily interrupts the general concavity of the surface and thereby produces two wide shallow grooves, one on either side. The part of the innominate bone between the pubic and anterior superior iliac spines, forms the floor of the pelvo-crural space. The anterior border of the abdominal surface of the bone presents four prominent landmarks:

1. The pubic spine.
2. The ilio-pectineal eminence.
3. The anterior inferior iliac spine.
4. The anterior superior iliac spine.

There are three concavities or grooves corresponding to the intervals between these, viz.:

1. A groove between the pubic spine and the ilio-pectineal eminence. The outer part of this is related to the femoral vessels and crural canal: the inner part to Gimbernat's ligament.

The origin of the pectineus muscle is also related to this area of bone.

2. A well-marked groove between the ilio-pectineal eminence and anterior inferior iliac spine.

3. A lesser marked groove or "notch" between the two anterior iliac spines.

These two grooves together lodge the ilio-psoas muscle. In a general way, the first mentioned and larger is devoted to the psoas: the second mentioned and smaller is allotted to the iliacus; but no hard and fast rule can be laid down. The muscles become inseparable below: usually part of the iliacus is found in the groove for the psoas.

*Poupart's ligament.* This is the lower edge of the aponeurosis of the external oblique muscle. It is free, but recurved so that it presents an abdominal concavity or gutter. Its inner and outer attachments are, respectively, the pubic spine, and the anterior superior iliac spine. This ligament—the upper boundary of the pelvo-crural space—is exceedingly strong, and is not quite straight, on account of its attachment to the deep fascia of the leg, which causes it to be slightly convex downwards and outwards.



Both the internal oblique and transversalis muscles of the abdomen take origin from its outer half.

*Gimbernat's ligament.* This is triangular with its apex at the pubic spine, and its base, free and concave, directed outwards. Its anterior border is attached to Poupart's ligament; its posterior border to about 1 inch of the inner extremity of the ilio-pectineal line. It acts as a strong barrier closing the inner inch or so of the pelvo-crural space.

*The ilio-psoas muscle.* The thin iliacus muscle arising from the greater part of the iliac fossa, and the much stronger psoas magnus muscle, coming from the sides of the lumbar vertebrae, fuse with one another below, and pass into the leg, to be inserted into the small trochanter of the femur (psoas) and into a smooth impression below this (iliacus). The area of bone between the ilio-pectineal eminence and the anterior superior iliac spine is covered by this combined muscular mass.

*Fasciae.* Each of the muscles just mentioned is covered by a dense and strong fascia, which is but little adherent to the underlying muscle. The fascia covering the iliacus is attached externally to the ilio-lumbar ligament, and the inner lip of the crest of the ilium. Internally it fuses with the fascia covering the psoas muscle and is attached to the lumbar vertebrae, sacrum and iliac portion of the ilio-pectineal line, below which it crosses the superior surface of the pubic ramus and is attached to the ilio-pectineal eminence.

This combined ilio-psoas fascia, as it follows the muscle into the leg, is united on either side of the muscle to the capsule of the hip joint and to the femur. As it passes beneath Poupart's ligament it is united to it by a number of tendinous intercrossing strands. At this point, too, I have noted, in dissecting in the post-mortem room, a number of very definite transverse fibres running from the anterior superior spine to the ilio-pectineal eminence. In effect therefore, there is a strong ligamentous or aponeurotic layer (nominally a part of the ilio-psoas fascia) attached on the one hand to Poupart's ligament and on the other to the ilio-pectineal eminence. This is called the ligamentum iliopectineum. The psoas parvus muscle, when it is present, will in some cases be found to be inserted partly into the ilio-pectineal eminence, thus fusing with and strengthening this ligament. In considering the anatomy of the femoral region, the ligamentum iliopectineum, sloping backwards and inwards towards its bony insertion as it does, may be conveniently used to subdivide the pelvo-crural interval into two lacunae. The outer and larger one, lying external to the ilio-pectineal eminence, and between it and the anterior superior iliac spine, is the *lacuna musculosa*. The smaller lacuna, internal to the ilio-pectineal eminence, and between it and the free concave edge of Gimbernat's ligament is the *lacuna vasculosa* (see fig. 1).

*Cooper's ligament.* This ligament was first described by Sir Astley Cooper. The best descriptions of it are those given by Testut (1), Poirier and Charpy (2), and P. Eisler (3).

M. G. Seelig and L. Tuholske (4), who have called attention to the fact,

that among anatomists, few seem to have realised the precise nature or indeed even the precise position of Cooper's ligament, have also produced a very excellent diagram illustrative of its position.

Cooper's ligament is a strong fibrous cord, which accurately overlies the pubic portion of the ilio-pectineal line from the pubic spine to the ilio-pectineal eminence. It therefore runs from the apex of Gimbernat's ligament to the ligamentum iliopectineum.

The basis or foundation of Cooper's ligament is the pectineal fascia. This passes upwards behind the femoral vessels and is inserted into the internal part of the ilio-pectineal line. Many other structures are inserted into this fascia just as it fuses with the periosteum at this point, and hence Cooper's ligament is formed from the pectineal fascia by the varying pull of all the other structures which are inserted into it. The structures which form Cooper's ligament are as follows:

1. The pectineal fascia.
2. Gimbernat's ligament.
3. The ligament of Henle (some muscle fibres of the transversalis abdominis running from the os pubis to the rectus abdominis).
4. The triangular fascia.
5. The ligament of Hesselbach (some muscle fibres passing from the transversalis abdominis to Poupart's ligament).
6. The conjoined tendon.
7. The lateral adminiculum of the linea alba.
8. The fascia transversalis.
9. The psoas parvus is in some cases prolonged into it.

Cooper's ligament thus constituted can be excellently seen in any case in the post-mortem room, from the abdominal side. It is important to realise what this ligament is, and where to find it, as it is made use of in closing the crural ring after femoral herniotomy. So strong and fixed is the ligament, that sutures passed through it can never "cut out," and the ligament will not "give," and so cause loosening of operation supports. The same properties



Fig. 1. Femoral region to shew measurements taken.

$AB$  = Poupart's Lig.  $AE$  = Gimbernat's Lig.  
 $BC$  = Ilio-Psoas (Lacuna Musculosa).  $AC$  = Pubic Spine to Ilio-Psoas.  $AC-AE=EC$  = Lacuna Vasculosa (Trans.).  $CF$  = Lacuna Vasculosa (Antero-Postr.).

cannot in every case be maintained with regard to other structures in the vicinity, which are frequently used for the strengthening suture. Judging by their behaviour, many operators consider the fascia over the pectineus to be Cooper's ligament.

*Lacuna musculosa.* This is so called because its main content is the ilio-psoas muscle. It also gives egress from the abdomen to two nerves of the leg, viz.:

1. The anterior crural nerve lying in the groove between psoas and iliacus.
2. The external cutaneous nerve of the thigh which lies just internal to the anterior superior iliac spine and crosses the notch below it.

These therefore both lie *behind* the ilio-psoas fascia.

*Lacuna vasculosa.* This has been so named as its main contents are the femoral vessels, which carry with them the so-called "femoral sheath."

The boundaries of the lacuna vasculosa are worthy of note.

*Anteriorly.* Poupart's ligament.

*Posteriorly.* Ascending ramus of pubis, covered in front by the origin of the pectineus, and overlaid along its posterior border by the pubic ligament of Cooper.

*Internally.* The unyielding edge of Gimbernat's ligament.

*Externally.* The ligamentum iliopectineum which is supported on its outer side by the muscular mass of the ilio-psoas.

The femoral sheath is formed (so we are told in all the anatomy books) of the fascia transversalis which lines the deep surface of the anterior abdominal wall, and of the fascia iliaca (ilio-psoas fascia). The femoral vessels lie upon the latter and are covered in front by the former. At the outer limit of the lacuna vasculosa these two layers fuse and are attached to Poupart's ligament. At the inner limit of the lacuna vasculosa, the fascia transversalis fuses with the periosteum of the pubis and with the pectineal fascia in the formation of Cooper's ligament, but at the same time it also fuses with the fascia iliaca and so a complete fascial funnel is said to be formed and prolonged into the leg. Two vertical partitions of fascia are described in the sheath giving rise to three compartments. The outer one contains the femoral artery and crural branch of the genito-crural nerve: the middle one, the femoral vein: the internal one except for lymphatics, fatty tissue, and sometimes a small lymph gland, is "empty" (i.e. occupied by tissue of small resistance) and constitutes the crural canal. It is here then that femoral hernia in the first place originates.

*The crural ring.* A description of this—the abdominal opening of the crural canal—brings us to the crux of the whole matter of femoral hernia. It lies at the level of Poupart's ligament, and is closed above by a condensation of extra-peritoneal fatty tissue (septum crurale) and by peritoneum which may be dimpled into it, forming what the older anatomists used to describe as the inferior digital fossa of peritoneum. The immediate boundaries of this ring are well known:

*Anteriorly.* Poupart's ligament.



*Posteriorly.* The pubis covered by the origin of pectineus.

*Internally.* The concave free edge of Gimbernat's ligament.

*Externally.* The femoral vein and artery.

The spermatic cord in the male (or round ligament in the female) and the inguinal canal in which it lies, both run downwards and inwards *in front* of the crural ring, but separated from it by fascia transversalis and also, maybe, by the conjoined tendon.

The deep epigastric artery lies somewhat to the outer side of and above the "ring."

The existence of the femoral sheath as at present described, is doubtful (see Part IV) and hence our account of the crural canal may be at fault. But what is quite certain is that a space exists between Gimbernat's ligament and the femoral vein. No doubt in the normal living body the femoral vein is very close to Gimbernat's ligament, and hence the space is obliterated or potential. When we examine this region in the dissecting room or the post-mortem room the vessels are either filled with injection or else collapsed and impressions made are likely to be false. When the same region is seen at a femoral herniotomy, an abnormal condition is observed. It is thus extremely difficult to say what is the normal condition of the femoral ring in a normal living individual. If we can, however, obtain some data as to the average size of these "rings" (post mortem) and their limits of extensibility, this information may be valuable in enabling us to elucidate the mystery of predispositions to femoral hernia.

## Part II

### FACTORS ARISING OUT OF COMPARATIVE ANATOMY AND MORPHOLOGY

Femoral hernia is of fairly frequent occurrence in the human species. De Garmo (5) states that 18 per cent. of all herniae are femoral, taking the two sexes together. He further avers that femoral hernia makes up 2.53 per cent. of all male herniae, and 35.15 per cent. of all female herniae. In the lower animals femoral hernia is of rare occurrence. Müller (6) speaks of its occasional appearance in dogs after a fracture of the pelvis. Veterinary surgeons of wide and extensive experience have announced that they have never seen a case. (Möller, Cadiot.) Inguinal hernia, on the other hand, is not an extreme rarity in animals in general. It is common in young equines, and though rare in ruminants and dogs it is common in bitches, especially those which have borne young. Keith (7) states that inguinal and femoral hernia occur so infrequently in mammals generally as to constitute them human peculiarities. It will be seen from what has already been said that this is especially true with regard to the femoral variety.

Something has occurred then in the later evolution of man which has rendered him more liable to femoral hernia. Mammalian evolution has occurred in a number of stages. Mammalian ancestors adopted the pronograde

posture and mode of progression: most mammals which we know are still in this stage. They move on four feet, the hind legs are at right angles to the trunk, and, as the balancing of the body is an easy process, the pelvic span is narrow.

A later phase in evolution is the orthograde stage, in which the trunk is maintained in an upright position during progression. Man and the higher primates—the anthropoid apes—make use of the orthograde posture. Man is, however, more highly evolved still. He has gone a stage further. Both he and the higher apes have adopted the upright posture, but he alone has adopted the plantigrade mode of progression; that is to say, he walks always upon the sole of the foot.

This last development has led to a complete opening out of the foot, leg, and thigh of such a nature that the lower extremity of man is of quite a different character from the lower or hind extremity even of the apes.

The opening out has, moreover, especially reacted upon the groin. The changes which have taken place in the muscular and fascial layer of this region have caused an enlargement of the communication between the abdomen and the thigh (which we have already referred to as the pelvo-crural interval). This necessarily means a weakening of this portion of the parietes of the abdomen. Besides all this, on account of a normally erect trunk, directly over a normally extended lower limb, (the two of them being constantly in one and the same straight line,) the weight of the abdominal contents and the force of gravity are able to act directly. Herein then lies the secret of the human predisposition to femoral hernia. The particular changes which have been involved in the adoption of the plantigrade posture and mode of progression by man, and which have led to his natural liability to femoral hernia are:

1. Changes in the external oblique muscle.
2. Changes in the attachments of the internal oblique and transversalis muscles.
3. Changes in the form of the pelvis.
4. The abdominal muscles have now a more direct action on the crural ring.

*The external oblique muscle.* This muscle is of a very different nature in the anthropoid apes from that obtaining in man. In the apes (and mammals in general) the muscle as it sweeps down from the lower ribs finds no attachment to any part of the ilium. The muscular part gives place to an aponeurotic tendon as in man, but this is inserted only into the pillars of the external abdominal ring and the body of the os pubis (see fig. 2).

In man the anterior superior spine and crest of the ilium, have, as it were, grown forward and cut into the external oblique, divorcing a large part of the muscular belly of the muscle from the aponeurotic part below. The muscular part now attached to the iliac crest has attained a new function in balancing the trunk and preventing it from rolling backwards on the heads of the femora.

The aponeurotic part in front of the iliac crest has taken on an increased strength in its lower part, (a reaction caused by the more permanent "push" of the viscera behind,) and has formed Poupart's ligament, which is therefore, in this highly developed form, peculiar to man. Certainly not more than the inner portion of this tendinous arch in man, is represented in other mammals.

*The internal oblique and transversalis muscles.* In all primates excluding man himself, these (conjoined) muscles have both a wider origin and wider insertion than in the human species. They arise from a large part of the fascia covering the ilio-psoas muscle, and also from the extensive anterior border of the ilium. Arching over the spermatic cord (or round ligament) in a sphincter-like manner, they have a fairly extensive insertion into the ilio-pectineal line.

In man these muscles do not arise from the fascial tunnel through which the ilio-psoas descends into the leg; nor yet from the anterior iliac border. They do, however, arise from the outer half of Poupart's ligament. It therefore becomes obvious that changes in the three muscles of the abdominal wall have

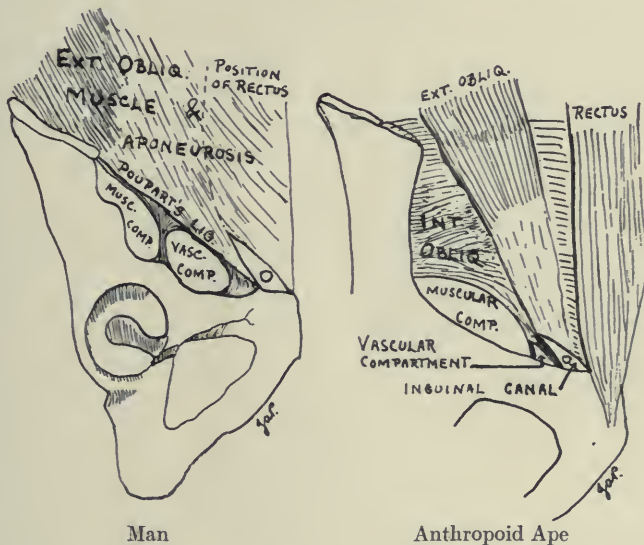


Fig. 2: Pelvo-crural interval in man and apes. (After Sir Arthur Keith—modified.)

a very far-reaching effect on the communication between abdomen and leg. By reference to fig. 2 illustrating a comparison between the femoral region of man and that of other primates it will be seen that the whole pelvo-crural interval in apes (i.e. lacuna musculosa and lacuna vasculosa) corresponds only to the inner half (i.e. little more than the lacuna vasculosa alone) of the same space in man. Furthermore, since the ilio-psoas muscle (and hence the lacuna musculosa) is roughly of the same relative size in both ape and man, it follows that the vascular compartment is of very considerably smaller dimensions in the anthropoids than in man. It seems then that since the main blood-vessels of the limb pass through this space, the likelihood of there being any surplus or



potential space to the inner side of the femoral vein, which might open out as a crural canal and permit a hernia to pass down, is very small in anthropoids, but more pronounced in the human species.

*The pelvis and abdominal wall.* Pronograde animals which walk on four legs balance their trunks easily. Their young at birth are small. For these two reasons we find that they have "long" pelves with a narrow span. As is natural a narrow anterior abdominal wall goes hand in hand with this. The plantigrade mode of progression which man has acquired demands a widened pelvis, in order that his feet may be able to support what would otherwise be a top-heavy trunk. The comparatively enormous size of the head of the full-term human child has also been responsible for a widening of the transverse diameter of the pelvis. The anterior abdominal wall has followed suit and widened out to a corresponding extent.

These changes have together led to an increase of the antero-posterior measurement of the pelvo-crural interval; or in other words Poupart's ligament, and the edge of the pelvis beneath it, are at greater distance from one another than are the corresponding structures in any other mammal.

Here again then the human susceptibility to femoral hernia is enhanced.

*The action of the abdominal muscles.* It has already been pointed out that in man the (erect) abdomen and (fully extended) lower limb are in one direct column, and that the force of gravity acting in the same direction, is a factor in causing tension (or "vis a tergo") upon the crural ring. The abdominal muscles will therefore, when they contract compress the abdominal organs, and cause these to exert still further "vis a tergo" upon a femoral ring, which has already been shown to be less secure in man than in animals (even anthropoid apes) on account of its greater diameter both antero-posteriorly and transversely in the human subject.

### Part III

#### FACTORS ARISING OUT OF THE ANATOMY OF THE FEMORAL REGION

When this work was being undertaken, it seemed likely to me that a comparison of a number of femoral regions in the two sexes, with a special reference to the absolute and relative measurements of Poupart's ligament and certain structures which occupied the interval between it and the bone, would throw some light upon the size (or at any rate the potential size, which is of far greater practical value) of the crural ring in male and female. The measurement of a series of innominate bones, from pubic spine to anterior superior iliac spine was made a preliminary to the study of the "soft parts."

#### BRIEF OUTLINE OF WORK DONE AND MATERIAL USED.

I. The measurements of 267 innominate bones classified according to sex were recorded. The measurement used was the distance from pubic spine

to anterior superior iliac spine: this is to all intents and purposes the measurement of Poupart's ligament.

II. Dissections of the femoral region, from the abdominal aspect with measurements of Poupart's ligament, Gimbernats ligament, and the breadth of the ilio-psoas as it leaves the abdomen, were made in 56 subjects,—on both sides of the body in each case. 54 subjects were obtained in the post-mortem room and 2 in the dissecting room. Results have, of course, been classified according to sex.

After the first 32 cases had been collected, it seemed to me advisable to obtain in the later dissections certain other measurements in addition, such as (1) the vertical depth of the space beneath Poupart's ligament at the inner border of the ilio-psoas, (2) the distance of the pubic spine from the inner border of the ilio-psoas, (3) in some cases the transverse measurement from the concavity of Gimbernats ligament to the inner border of the (collapsed) femoral vein.

The interspinous and intertubercular (transverse) measurements of the pelvis were also noted in these later cases.

For these reasons, the 56 cases referred to have been divided up into two series as follows:

<i>Series I.</i>	Cases 1-32	{ 21 males
	(32 cases)	{ 11 females
<i>Series II.</i>	Cases 33-56	{ 12 males
	(24 cases)	{ 12 females

III. Measurements of the interspinous and intertubercular distances were made on the pelvis of 50 living subjects. 25 of these were male and 25 female. (Similar measurements were afterwards made on post-mortem subjects in Series II.)

IV. Measurement (or more correctly indirect calculation) of the size of the angle at the pubic spine, between Poupart's ligament and the pubic ramus was made from 12 male and 12 female disarticulated innominate bones, by a device of projecting this angle and its boundaries on to a piece of paper in each instance.

In an analysis of the records of 100 unselected cases of femoral hernia, operated upon in one unit of the Manchester Royal Infirmary, made by me, the following large disproportion of its incidence in the two sexes was observed:

100 cases of femoral hernia.	Males	19
	Females	81
	Total	100

This enormous disparity, representing, in this series, a ratio of 1 : 4.25 between males and females, caused me to think that variations in the size of anatomical structures in the vicinity of the crural canal might be discovered which would explain these figures.

## I. EXAMINATION OF 267 INNOMINATE BONES.

All the bones which could be found in the anatomy department (both modern and Egyptian) were used, as well as a few privately owned innominate bones.

*Technique.*

The object in view was to classify the bones according to their sex, and then to measure the distance between the spine of the pubis and the anterior superior iliac spine. This distance, it will be seen, is the same as that of Poupart's ligament, which is attached to these bony points, and the measurement will therefore represent the transverse or longest diameter of the pelvo-crural interval.

The first problem which had to be faced was the difficulty of classifying the bones correctly as to their sex. The majority of the bones were merely disarticulated innominate bones. In some cases they were in pairs from the same skeleton, but still separate from one another. In a few instances complete articulated pelves were obtained and four or five complete skeletons also contributed to the series. In the main, however, one had to consider the best way of diagnosing the sex of an isolated innominate bone. The following table shows the points which I found most useful in distinguishing a female os innominatum from a male one:

*Differences of female os innominatum from that of male.*

1. It is lighter and less massive.
2. It is smoother.
3. The muscular attachments have left less well-marked impressions behind them.
4. The pubic arch is low, wide and rounded—at least  $90^\circ$  (in the male  $65-70^\circ$ ).

This had to be estimated by placing the bone in its normal position in the body so that the symphysis was roughly vertical, and the front of the bone faced the observer, and then placing a finger, of whichever hand was suitable (according as to the side of the innominate bone) in the position of the pubic and ischial rami of the opposite side. In this way the size of the subpubic angle could be estimated by the eye.

5. The pubic symphysis is less deep.
6. The pubic body is wider in the transverse diameter.
7. The obturator foramen is smaller and more triangular.
8. The acetabulum is proportionately smaller.
9. The great sacro-sciatic notch is wider and shallower.
10. A pre-auricular groove is found on some but not all female bones just in front of the auricular surface.
11. The tuberosity of the ischium is more everted (in many cases this would be better described as "less inverted").
12. The ischial spine is less inverted.



It cannot be maintained that any one of these "differences" can be taken as infallible, but each bone had to be considered upon its own merits. The tenth point, the shallow smooth groove just in front of the rough auricular surface, described by Derry (31), has in some cases of difficulty proved to be a valuable aid in establishing the sex of a bone.

The second difficulty which arose was how to make the measurement correctly. For this purpose a pair of metal calipers was used. It consisted of a metal scale in centimetres and millimetres, with two pointers at right angles to the scale. One of these pointers was fixed at one end of the scale, the other was arranged so that it could be moved up and down along the ruler. For accuracy of measurement, both arms were pointed at their extremity in such a way that the distance of their points from one another could be easily read off on the scale.

The pubic spine, since it is of no great size and usually *does* present a more or less pointed extremity, adapted itself readily in most cases to direct and accurate location by the point of the calipers. The anterior superior iliac spine, however, was less easy to reduce to a "point." This bony eminence is of moderate size, and in some instances is about an inch long from without inwards in continuation of the iliac crest. It is then very doubtful if the term "spine" is applicable to it at all. In those cases where a definite pointed projection or spine of bone has been found in this vicinity, the point of the calipers has been set upon it: in cases where an "eminence" rather than a "spine" of bone has been encountered, the point of the calipers has been placed upon that part of it where the curvature is at its maximum.

It is felt that this usually represents its "spine," and that one observer in going through a series of a large number of bones, will grow used to locating the summit of a somewhat diffuse "spine" at a point which corresponds in all members of the series.

By means of these devices a series of measurements has been obtained from 107 modern bones and 160 ancient Egyptian bones (derived from the collection of Egyptian remains made by Professor G. Elliot Smith). The numbers of each sex were as follows:

*Innominate Bones.*

<i>Modern</i>	Male 73	Female 34	Total 107
<i>Egyptian</i>	Male 85	Female 75	Total 160
	158	109	267

Only adult ossa innominata have been measured, i.e. those which were at or beyond the age of 20-25 years, and in which therefore the ilium, ischium and pubis had united.

*Results.* The results of the 267 measurements from pubic to anterior superior iliac spines, after having been classified, tabulated, and averaged out, yield the following interesting results:

Table A. *Ossa innominata*. Distance from pubic spine to anterior superior iliac spine.

<i>Ossa innominata</i>	No. of cases	Variation (cms.)	Average (cms.)
Male (Modern) ...	73	9.6 to 13.6 = 4.0	12.0
Female (Modern)	34	10.3 to 13.9 = 3.6	11.8
Male (Egyptian)	85	10.0 to 13.8 = 3.8	11.5
Female (Egyptian)	75	9.3 to 13.2 = 3.9	11.0

It may be pointed out here that the above figures, and all the measurements recorded in this thesis, are in centimetres.

In those cases where pairs of bones have been measured the two sides are usually but not always in exact agreement with one another. The difference has usually only amounted to two or three millimetres but has, in one or two cases, reached nine millimetres or about a centimetre. At the time of measurement, I observed these differences, and, on investigating their cause, I found that the general conformation of the innominate bone on the two sides differs in some cases, while in others differences of the size, shape, and even the position of the pubic or anterior superior iliac spines were responsible for the inequality of the measurements of the right and left bones.

The main points of interest are as follows (see above table):

1. *The pubo-iliac distance* (such we shall hereafter designate this measurement from pubic spine to anterior superior iliac spine) *is definitely larger in the male than in the female*. So, then, is Poupart's ligament. The average distance is in the modern male bone 12.0 cms., and in the modern female 11.8 cms. That is to say, the pelvo-crural interval is 2 mm. wider on each side of the body, on the average in the male. The corresponding measurements of the male and female Egyptian bones are 11.5 cms. and 11.0 cms., representing an average increased width of half a centimetre on each side of the male body.

2. The average pubo-iliac distance is greater in modern than in Egyptian bones, comparing them sex for sex; being respectively 5 mm. greater in the male and 8 mm. greater in the female. This suggests that modern man may be becoming more susceptible to femoral hernia than were his ancestors. One cannot, however, do more than suggest this as an interesting possibility. (It has already been shown that the processes of later evolution tend towards an increase in the predisposition to femoral hernia.) Racial or statural differences, of which we are unaware, creep in, on the other hand. Hence it is unwise to dogmatise on this point.

3. The extreme limits of variability of this measurement are to be noted. The smaller figure given in the "variation" column of the table, is the smallest measurement recorded; the bigger one, the greatest, in the sex and series under consideration. It will be seen that in each sex (whether modern or ancient bones are considered) the extreme limits of variability amount almost to 4 cms.

4. The fact that the pubo-iliac distance is not always quite the same on the two sides of the body has been already pointed out and commented upon.

Cleland (9) has investigated the iliac divarication in a series of cases, i.e. the angle which the anterior borders of the ilia of opposite sides make with one another. He states that there is considerable variation in the angle at which the right and left bones lie to one another, but that the variation does not depend on sex.

In a series of adult bones he has found the following to be the extreme limits in the angle of divarication:

Male  $16^{\circ}$ – $89^{\circ}$  (average angle  $53^{\circ}$ )

Female  $22^{\circ}$ – $81^{\circ}$  (average angle  $50\frac{1}{2}^{\circ}$ ).

He has further pointed out that this divarication is large in childhood and diminishes until early adult life, after which it again tends to increase.

It seems likely, then, that this variable angle of divarication of the ilia is intimately bound up with the large degree of variability of the pubo-iliac measurement, which has been shown under paragraph (3).

Similarly slighter degrees of asymmetry of this angle will account for the minor differences noted in the measurement of the pubo-iliac distance on the two sides of the same skeleton, which has been already referred to under paragraph (4).

## II. DISSECTION AND EXAMINATION OF THE FEMORAL REGION IN 56 SUBJECTS.

The important fact culled from the examination of the dried innominate bone was that the female pubo-iliac measurement (and therefore, presumably, the female Poupart's ligament) is shorter than the male one. The average diminution ranges from 2 mm. in modern to 5 mm. in ancient Egyptian bones.

If an alleged wider pelvis is responsible for the great female predisposition to femoral hernia is it not somewhat surprising that the actual space under Poupart's ligament (transversely, of course) should be less in women than in men? If it can be shown that this measurement in women is relatively as well as absolutely shorter, then will the time-honoured "wider pelvis theory" of femoral hernia crumble to pieces.

Since an examination of bones alone would not suffice to explain female susceptibility, the next thing was to turn to an examination and comparison of the "soft parts" which pass under Poupart's ligament.

This as already indicated has been carried out in 56 subjects on both sides of the body, and is then the equivalent of the examination of 112 femoral regions. 54 of these cases were examined in the post-mortem room, and 2 in the dissecting room.

### *Technique.*

The theoretically obvious thing to do, in examining the soft parts with a view to elucidating the etiology of femoral hernia, with its disproportionate



sexual incidence, was to measure the crural ring in the two sexes. This, however, is impracticable, since its outer boundary (the femoral vein and artery) is collapsed in post-mortem room subjects, and artificially distended by injection in dissecting room subjects. Gimbernat's ligament (its inner boundary) it is true, is reasonably fixed. One finds in practice, that within reasonable limits, a measurement of the transverse diameter of the "crural ring" can be made anything which the measurer cares to make it. I have, at times, been persuaded to make this measurement. I have never based much reliance upon the figures obtained.

Therefore some other method of arriving at its measurement, or better, limits of measurement had to be devised. It seemed wise to measure first of all, those structures beneath Poupart's ligament which had fixed and reliable borders, so that trustworthy figures might be obtained. The following were resolved upon (see fig. 1).

*Length of Poupart's ligament* (fig. 1 *AB*). This was found by placing the points of the calipers upon the two ends of this ligament, at its attachment to the pubic spine and anterior superior iliac spine, respectively. It should be noted that this is the same measurement as that obtained from the dried bones.

*Transverse measurement of Gimbernat's ligament* (fig. 1 *AE*). One point of the calipers upon the pubic spine, and the other upon the centre of the concavity of the free edge of this ligament, gave the required reading. In actual practice it was often found easier to use, not the points of the calipers but the arms of the calipers about half an inch from the points. Since the points were flush with the opposing borders of the arms of the calipers, this made no difference in the measurement, except that one had to make certain that the scale was parallel with the long axis of Gimbernat's ligament, in order to avoid an oblique measurement which would otherwise stultify the result.

*The breadth of the ilio-psoas mass, as it passes beneath Poupart's ligament* (fig. 1 *BC*). For this measurement one pointer of the calipers was placed on the anterior superior iliac spine, and the other on the attachment of the ilio-psoas fascia to the ilio-pectineal eminence, *at the level of Poupart's ligament*. The last phrase is important. This latter fixed point corresponds with the insertion of the ligamentum ilio-pectineum into the bone, and it will be seen that the measurement represents the transverse diameter of the lacuna musculosa.

In the first 32 cases (including 21 male subjects and 11 female subjects), these measurements alone have been recorded, except that in seven of these cases the antero-posterior and transverse measurements of the crural ring have been taken on one or both sides of the body. The age of each patient has been noted where it was known. In two or three cases where it was not known, the approximate age has been estimated after an examination of the subject.

These first 32 cases in which the three measurements indicated were alone obtained have been tabulated and recorded separately from those cases which

followed, as at this stage in the work it seemed to me advisable to record some other measurements in addition.

To distinguish these two series of cases from one another they have been designated:

*Series I.* Cases 1-32: comprises 21 males and 11 females; and

*Series II.* Cases 33-56: comprises 12 males and 12 females.

The new measurements (see fig. 1) were included in an effort to get data which would more directly act as indices of the transverse and antero-posterior diameters of the crural ring. They are as follows:

*The antero-posterior measurement of the lacuna vasculosa at the inner border of the ilio-psoas* (fig. 1 *CF*). This is measured by placing the scale of the calipers vertically so that one pointer is touching the bone at the place where the ilio-psoas fascia is inserted into it (and of course at the level of Poupart's ligament). The other pointer, which must lie vertically above the first one, is adjusted until it just touches Poupart's ligament. The subject, of course, lies upon the back on the table, hence this "vertical" measurement so taken, becomes converted into an antero-posterior measurement in the anatomical posture. It is to be remarked that this measurement, *CF* in fig. 1, although not a direct measurement, is an index of the antero-posterior diameter of the crural ring.

*A measurement from the pubic spine to the inner border of the ilio-psoas* (at the level of Poupart's ligament) has also been taken. This is *AC* in fig. 1. The line of this measurement, it will be seen, cuts across the centre of the free edge of Gimbernat's ligament at the point *E*, and the measurement of Gimbernat's ligament (*AE*) has already been taken. By a simple subtraction, therefore, the measurement *EC* can be found and in this way another measurement has been adduced, viz.:

*The transverse diameter of the lacuna vasculosa* (fig. 1, *EC*). Assuming that the calibre or diameter of the femoral vein and artery in the adult, in the two sexes and at various ages, only vary within limits which are so small as to be negligible, this measurement may be taken as an index of the transverse diameter of the crural ring. In Series II., I have again, in a few cases, been tempted to measure the transverse diameter of the crural ring directly (i.e. from centre of concavity of Gimbernat's ligament to the inner border of the (collapsed) femoral vein). As before pointed out, this is scarcely a reliable measurement.

I have also measured the interspinous and intertubercular diameters of the false pelvis in Series II.

These measurements of structures passing under Poupart's ligament have been effected from the abdominal side. All the post-mortem cases have been seen for the first time by me after an ordinary post-mortem examination had been carried out. The abdomen was found open by the median incision, some or all of the abdominal and pelvic viscera were usually found removed. The

femoral region was in most instances not interfered with in the slightest. The *modus operandi* has usually been as follows:

Extending the median incision downwards over the pubic symphysis, I turned outwards the right-hand flap of the abdominal wall in one layer, so that I could see its deep surface. From its cut edge, I now dissected the rectus abdominis cleanly from the anterior part of its sheath, which appears as an opaque white aponeurosis. Having dissected in this plane as far as the outer border of the rectus, and a little further if possible, I make an incision through the aponeurosis of the internal oblique, parallel to the outer border of the rectus in its lower part. This incision, with the abdominal wall in the everted position, also corresponds roughly with the line of Poupart's ligament. The above incision is only made about half an inch in length at first. If the aponeurosis of the external oblique muscle, near the point at which it becomes Poupart's ligament, is seen (as it usually is) the incision is extended widely up and down, and the internal oblique aponeurosis is dissected off and pushed back. The everted external oblique aponeurosis and Poupart's ligament are soon thoroughly exposed from within, and the lower part of the internal oblique muscle is seen arching downwards and inwards in its normal situation.

The spermatic cord (or round ligament) is cut and turned aside. Beneath it is the crus inferius of the external abdominal ring and the inner part of Poupart's ligament. Turning back that part of the abdominal wall which still remains *in situ* (internal oblique, transversalis, and rectus) the peritoneum is removed from Gimbernat's ligament, and the crural ring defined.

I have, in most cases in my series, dissected and examined the obturator arteries and veins (normal or abnormal) and their anastomoses and communications (especially venous). To facilitate this dissection, I have usually half cut through the attachment of the rectus to the os pubis, as by this means a better view of the pelvic cavity may be obtained.

These vessels having been examined, the pubic spine and anterior superior spine are well defined and Poupart's ligament and Gimbernat's ligament measured as already indicated. The scissors are now run along the upper border of the os pubis and Poupart's ligament and the rectus, internal oblique and transversalis muscles severed from these structures. The transverse diameter of the crural ring where recorded has been noted at this stage, after which the external iliac vessels have been cut at the level of Poupart's ligament where they become continuous with the femoral vessels, and turned up out of the way. The junction of ilio-psoas fascia with the bone is well defined, and the breadth of the ilio-psoas noted. In Series II the antero-posterior measurement of the lacuna vasculosa, and the distance from pubic spine to inner border of ilio-psoas, are also recorded at this stage. The presence or absence of the psoas parvus muscle and its mode of insertion, have usually been noted.

In a certain number of the later cases of Series II and where the peritoneum had not been removed or destroyed, I examined for peritoneal diverticula at



the femoral and inguinal rings. These will be referred to later. In dissecting room subjects I have had to wait until the dissection of students reached a suitable stage, and then clean up the parts concerned and take the required measurements. As I found this less satisfactory than the fresh post-mortem room cases, only two dissecting room subjects were included. Throughout, only adult subjects have been used.

### *Results.*

Series I will be first considered. In nearly all bilateral measurements, minor differences have sometimes arisen on the two sides. Totals and averages have been worked out for both sides of the body. In the following tables which represent results summarised, the limits of variation (shortest and longest measurements) as well as the average measurement of each structure in the two sexes have been shown. The figures in brackets are averages of left side measurements.

Table B. *Series I. Males. 21 cases.*

Measurement of:	Variation (cms.)	Average (cms.)
Poupart's ligament	9.5 to 13.1 = 3.6	11.84 (11.81)
Gimbernats's „	1.1 to 2.7 = 1.6	2.03 (2.03)
Ilio-psoas ... ..	6.2 to 9.7 = 3.5	8.10 (8.11)

Table C. *Series I. Females. 11 cases.*

Measurement of:	Variation (cms.)	Average (cms.)
Poupart's ligament	10.4 to 13.4 = 3.0	11.44 (11.43)
Gimbernats's „	1.4 to 2.7 = 1.3	2.13 (2.03)
Ilio-psoas ... ..	6.7 to 9.1 = 2.4	8.04 (7.95)

In the table below, the average measurements in the two sexes are compared (figures are in centimetres):

Table D.

Series I	Poupart's lig. (cms.)	Gimbernats's lig. (cms.)	Ilio-psoas (cms.)
Male averages	11.84 (11.81)	2.03 (2.03)	8.10 (8.11)
Female „	11.44 (11.43)	2.13 (2.03)	8.04 (7.95)
Difference and in which sex greater ...	0.40 (0.38) male greater	0.10 (0.00) female equal greater	0.06 (0.16) male greater

It will be seen in the first two tables above (B and C) that the respective lengths of the ligaments of Poupart and Gimbernats, and the breadth of the ilio-psoas all vary within wide limits. This is especially true of Gimbernats's ligament, though its measurement is usually in the close vicinity of 2.0 cms.

In the last table given (D), a comparison of male and female averages in Series I, both on the right and on the left (bracketed) side, has been shown. The points for observation are:

*Poupart's ligament.* The measurements agree remarkably with those obtained from the dried bones. The male ligament exceeds the female one by

4 mm. on the average (in the modern bone measurements it exceeded by 2 mm.: in the Egyptian by 5 mm.).

*Gimbernat's ligament.* The female average exceeds the male on the right side measurements by 1 mm. only: the left side measurements are in perfect agreement and show the sexes to be equal. We conclude therefore that on the average *sexual differences in the length of Gimbernat's ligament are negligible.* This ligament is usually 2 cm. long.

*Ilio-psoas.* This muscular mass is on the average very slightly wider in the male than the female. The larger excess is shown on the left and is only 1.6 mm. which at first sight tempts us to suppose that sexual differences in the breadth of this muscle are negligible.

Let us turn now to results obtained in Series II. As before, left side measurements or averages, where they differ are placed in brackets after the right side figures.

Table E. *Series II. Male. 12 cases.*

Measurement	Variation (cms.)	Average (cms.)
Poupart's ligament ... ..	10.8 to 13.2=2.4	12.04
Gimbernat's ligament ... ..	1.2 to 3.0=1.8	2.03 (2.00)
Ilio-psoas ... ..	7.6 to 9.6=2.0	8.84
Crural ring (transverse) (? reliable)	1.0 to 2.4=1.4	1.57
Lacuna vasc. (antero-posterior) ...	0.9 to 2.0=1.1	1.31
Pubic spine to ilio-psoas ... ..	3.9 to 5.1=1.2	4.31
Lacuna vasc. (transverse) ... ..	1.4 to 2.8=1.4	2.28 (2.30)

Table F. *Series II. Female. 12 cases.*

Measurement	Variation (cms.)	Average (cms.)
Poupart's ligament ... ..	10.5 to 13.5=3.0	11.57
Gimbernat's ligament ... ..	1.4 to 2.7=1.3	2.05 (1.96)
Ilio-psoas ... ..	7.0 to 9.9=2.9	8.04 (8.06)
Crural ring (transverse) (? reliable)	1.0 to 2.1=1.1	1.50 (1.52)
Lacuna vasc. (antero-posterior) ...	0.9 to 1.8=0.9	1.20
Pubic spine to ilio-psoas ... ..	3.8 to 5.3=1.5	4.77 (4.75)
Lacuna vasculosa (transverse) ...	2.0 to 3.9=1.9	2.72 (2.78)

Very similar degrees of variation are shown here as were observed in Series I. A comparison of the average measurements of Series II in the two sexes and on the two sides (where they differ to any degree) is shown in the table below (the figures are in centimetres):

Table G.

Series II	Poupart's Ligament	Gimbernat's Ligament	Ilio-psoas	Crural Ring	Lacuna Vasculosa (antero-postr.)	Pubic Spine to Ilio-psoas	Lacuna Vasculosa (trans.)
Male averages ...	12.04	2.03 (2.00)	8.84	1.57	1.31	4.31	2.28 (2.30)
Female averages	11.57	2.05 (1.96)	8.04	1.50	1.20	4.77	2.72 (2.78)
Difference and in which sex greater	0.47 greater	0.02 female greater	0.80 male greater	0.07 —	0.11 male greater	0.46 female greater	0.44 (0.48) female greater

All measurements are in centimetres.

The points for observation in Series II are considered below:

*Poupart's ligament.* The figures agree very remarkably with those obtained in Series I and also with the bone measurements. We may take it as an established fact that the male Poupart is on the average 4 mm. longer than the female.

*Gimbernat's ligament.* Series II only confirms Series I. It is shown that *no definite sexual variation of this ligament occurs*. By an infinitesimal amount the female measurement exceeds that of the male on the right side. On the left the reverse is true.

*Ilio-psoas.* The average male breadth of this muscle in Series II exceeds that of the female by as much as 8 mm. Series I showed a male excess of about 1.6 mm. It is plain, therefore, that the female ilio-psoas is very definitely narrower than the male. The average absolute diminution is somewhere between 1 and 8 mm., an amount which is by no means negligible as Series I alone suggested.

The maximum sexual difference in the breadth of the ilio-psoas muscle is 8 mm. The sexual difference in the length of Poupart's ligament is 4 mm. The female measurement is in both cases the lesser one. Considering the fact that in absolute length the ilio-psoas measurement is only about two-thirds of the Poupart measurement, it is evident that *the average breadth (and size) of the female ilio-psoas is relatively as well as absolutely smaller than its male counterpart*. This is a fact which we can in no wise disregard, as its meaning is that the lacuna vasculosa is correspondingly wider in the female.

*Lacuna vasculosa (transverse measurement).* How this has been arrived at has already been shown. It is the measurement from pubic spine to inner border of ilio-psoas *minus* length of Gimbernat's ligament. The figures show a very definite average increase in the female on both sides of the body. This increase amounts to between 4 and 5 mm. It must obviously be the result of the smaller female ilio-psoas which has just been referred to.

Now there cannot be much sexual difference in the diameter of the femoral artery and vein. If there is any, the female vessels are likely to be narrower. Suppose we assume each vessel to be 8 mm. wide in each sex, then the two vessels side by side occupy a space of 16 mm.; but the whole lacuna vasculosa is 23 mm. wide in the male, and 27 mm. wide in the female. This leaves an average transverse diameter for the crural ring of 7 mm. in the male and 11 mm. in the female. The crural ring is considerably wider then in the female, and if the calibre of vessels in the female is less than in the male, then is the female crural ring still greater relatively to that in the male. It should be noted that the *relative excess of this measurement in the female is greater even than the absolute excess* (on account of a shorter Poupart's ligament). It has been frequently pointed out that direct measurements of the crural ring (transversely) are inaccurate and to be avoided. They are given in the table above for what they are worth, and also to illustrate their inaccuracy. From these figures one would infer that the crural ring is equal (about 1.5 cm.) in the two sexes.



I have only shown the relatively greater size of the female crural ring (transversely) which is consequent upon a relatively smaller female ilio-psoas. Concerning its *absolute size* in the two sexes I wish to say nothing on account of the great difficulties of accurate measurement. De Garmo (5) states that Hesselbach has given this measurement as 10 mm. for the female and 5 mm. for the male crural ring. Berry (10) gives its transverse measurement as "about 1.2 cm." qualifying his statement by saying that it is larger in the female. I am of the opinion that it is unjustifiable to give absolute measurements of the crural ring unless one works over an immense series of cases, or is able to devise some means of reducing the truly enormous coefficient of error.

*Measurement of the lacuna vasculosa (antero-posteriorly).* In the table given the male figure is shown to be in excess by about 1 mm. It appears that the sexual difference of this distance is negligible, in which case the antero-posterior measurement of the crural ring (of which the above is taken as an index) must be also indifferent in the two sexes.

### III. MEASUREMENT OF 25 MALE AND 25 FEMALE PELVES IN THE LIVING.

When it was first discovered that the average female Poupart's ligament was 4 mm. shorter than the male, I began to doubt if the female pelvis was really wider than the male after all. The false pelvis is, of course, referred to. I made a search for actual measurements of a series of interspinous and intertubercular (pelvic) distances in males and females. As I could find no such record, I proceeded to measure 25 pelves of each sex in the living subject. Cases were not in any way selected. Three of the female cases were in hospital for a right-sided femoral hernia.

#### *Technique.*

A pelvimeter was used of an exceedingly simple type. It consisted of two curved metal blades riveted together and it possessed no scale. The rivet was firm enough to prevent the blades from moving accidentally when the instrument was removed from the pelvis. The measurements were read off in centimetres on a separate flat scale placed upon any level surface. All patients were measured while lying flat on the back. Three measurements were taken in each case:

1. *The interspinous distance* measured from a point directly *over* the anterior superior iliac spine of one side to a similar point on the opposite side.
2. *The interspinous distance* measured from a point *immediately to the outer side* of the anterior superior iliac spine of one side to a corresponding point on the opposite side of the body.
3. *The intertubercular distance* (widest diameter of false pelvis) measured from the outer side of the tubercle on the iliac crest, about  $2\frac{1}{2}$  inches behind the anterior superior spine, of one side, to the corresponding point on the opposite side.

*Results.*

Sunmarised results only are given here:

Table H. *Measurement of 25 male and 25 female pelves. Averages.*

		Average age of 25 cases	Interspinous distance (over spines)	Interspinous distance (outer side of spines)	Intertubercular distance
Males	...	28.67 years	23.50 cm.	25.94 cm.	28.50 cm.
Females	...	41.24 „	23.74 „	25.90 „	28.07 „
Difference and in which sex greater	...	12.57 „	0.24 „	0.04 „	0.43 „
		Female greater	Female greater	Male greater	Male greater

According to these results, *at the spines* of the ilia the female pelvis is  $2\frac{1}{2}$  mm. wider than the male, i.e., each half of the female pelvis is  $1\frac{1}{4}$  mm. wider than its male counterpart. It is upon this  $1\frac{1}{4}$  mm. which the “wider pelvis theory” of femoral hernia, to account for it being more frequent in the female, is built up!

The interspinous measurement taken *at the outer sides* of the iliac spines is to all intents the same in the two sexes: the intertubercular measurement is 4 mm. greater in the male than the female.

After I had taken these measurements, I also took the same measurements upon all the post-mortem subjects in Series II (12 males and 12 females). There is no reason to suppose that these measurements should be any different just after death. The sexual differences between the mean measurements in this series are:

Interspinous (*over spines*), 8.9 mm. (male greater).

Interspinous (*outer side*), 6.5 mm. (male greater).

Intertubercular, 7.6 mm. (male greater).

The interspinous distances measured *over* the spines are not in agreement in the two series: in one the female measurement is in excess by  $2\frac{1}{2}$  mm. and in the other the male by 9 mm.!

This requires some explanation. Cleland's (9) contention that the angle of divarication of the iliac blades decreases till early adult life, and then increases again owing to muscular action (glutei muscles in walking), has already been referred to. In the comparison of 25 male pelves with 25 female ones, the average female age was 41 years (i.e. past early adult life), but the average male age was only 28 (i.e. *at* early adult life). Hence the angle of divarication in the male bones was at its minimum. This fact has allowed the female interspinous distance to preponderate over that of the male. We should expect that in a more elderly male series, time for the divarication of the blades having been allowed, the male measurement at the spines would easily exceed the female—and so it does in the comparison of 12 subjects (post-mortem) of each sex which has been referred to. The males in the latter series are much more elderly (average age is  $42\frac{3}{4}$  years): hence the male excess of nearly a centi-

metre. It should, of course, be remembered that the female false pelvis is relatively wider than it seems, on account of the shorter stature of the female skeleton.

Even when the above results are all added together and averaged out and the sexes compared, so that 37 male pelves are compared with 37 female ones, we still find that all the three measurements are in excess in the male: but the male interspinous distance (*over* the spines) only exceeds by 1 mm., while the male intertubercular distance exceeds by 5 mm.

In pondering over these results it has seemed to me exceedingly doubtful whether the female (false) bony pelvis is wider than the male pelvis after all, —at the anterior superior spines, is, of course, meant. There is no doubt whatsoever, but that the male pelvis is both absolutely and relatively greater at the tubercles (from the figures given).

With the interspinous distance we are in a difficulty. When the cases are about the same age the sexual difference of the mean figures of this distance (9 mm.) is greater than that of the intertubercular distance (7 mm.), whereas in other cases (e.g. where 37 subjects of each sex are compared) it is much less (1 mm.). The first of these statements causes us to insist on the fact that the male interspinous distance is both absolutely and relatively greater than the female: the second statement makes us wonder whether we ought to include the word “relatively.” On the whole the evidence is in favour of its inclusion. Since we are quibbling over a distance only amounting to one or two millimetres in the transverse interspinous diameter, the relative difference must be very small irrespective of the sex in which it is greater. Judging from these figures it seems to me that if the male interspinous distance is not relatively greater than the female it must be relatively equal to it for all practical purposes, since any female excess could only be greater by an infinitesimal amount.

We have shown that the female interspinous distance is either relatively and absolutely smaller than the corresponding male measurement or else for all practical purposes that measurement is relatively equal in the two sexes.

Frazer (8) states that the female ilium is more vertical than the male, and that the female false pelvis is therefore relatively narrower.

This is an important observation. It is the final death-blow at the “wider pelvis theory” of femoral hernia, for we have now proved that the female false pelvis in general (and its interspinous distance in particular) is, relatively, *not* wider than the male false pelvis (and its interspinous measurement). On the contrary it is relatively narrower than, or at most only just equal to the male distance.

The female true pelvis *is* indeed larger than the male. This has in times past blinded our eyes, until the wider female pelvis has become traditional. Stress therefore needs to be laid on the fact that the female *false* pelvis is *not* wider than that of the male.



IV. MEASUREMENT OF THE ANGLE BETWEEN POUPART'S LIGAMENT  
AND THE BONE.

In the earlier part of this research, when there seemed to be but small and inconclusive evidence of a transversely wider female crural ring, it occurred to me that perhaps the female antero-posterior measurement of that ring was definitely greater than in the male. This possibility was still further strengthened by a remark made by me to Mr Geoffrey Jefferson. He told me that in operating upon a number of femoral herniae, he had noted that the angle, made by Poupart's ligament and the ilio-pectineal line, appeared to be greater in female than in male subjects. The outcome of this was, that I sought some means of estimating the actual size of this angle.

*Technique.*

In undertaking to measure this angle many difficulties at once presented themselves. For instance, the pubic bone is not quite straight at the ilio-pectineal line, and the surface of bone in front of this line (near the anterior border) is much curved in the formation of a marked concavity. Secondly, in the relaxed condition of the soft parts, seen in the post-mortem room after partial reflection of the abdominal wall, Poupart's ligament is slackened and movable within limits.

It occurred to me that the simplest method would be to take the dried and disarticulated innominate bone in a series of cases, and endeavour to project the pubic spine, anterior superior iliac spine, and the inner 3 inches of the ilio-pectineal line on to a piece of paper. Neither is this method without its difficulties. I have, however, been able to obtain the desired angle (which I have designated the inguino-pectineal angle) in the following way:

*Method I. (Measurement of the inguino-pectineal angle.)* Taking an innominate bone, and holding it so that its acetabular cavity faced directly upwards, I have placed the bone on a piece of white paper lying on the table, in such a way that the greater part of the expanded and curved ilium projected over the edge of the table towards me (see Plate I, fig. 1). This was done in order to get the pubic and iliac spines and the ilio-pectineal line all as flat as possible on the table. They cannot, of course, be got absolutely flat. Having got the bone in as suitable a position as possible, it has been my custom to hold it firmly in position (Plate I) with my left hand, and, looking directly down from above over the points mentioned, to project on to the underlying paper, and mark with a pencil the position of, first the pubic spine, and second the anterior superior iliac spine. After this, the pencil is run along the inner 3 inches of the ilio-pectineal line, which is thus projected on to the paper. The bone is now removed, and the points marking pubic and iliac spines are joined up in a straight line by a ruler. A reference to fig. 3 (I), shows the result obtained. Point *A* represents the iliac spine; point *B* the pubic spine; the straight line *AB* represents Poupart's ligament; the curved line *BDC* is the projection of the ilio-pectineal line. The angle *ABC* in this diagram will

therefore represent the inguino-pectineal angle (the inner angle of the pelvo-crural interval).

But how is one to measure an angle, one side of which is an unevenly curved line? This difficulty has been surmounted by the following device. From measurements obtained it has been shown that Gimbernat's ligament occupies usually the inner two centimetres of the pelvo-crural space. Next to it comes the crural ring, the dimensions of which are not accurately known. A centimetre and a half has, however, been allowed for its breadth. The allowance of  $3\frac{1}{2}$  cms. from the pubic spine will, we presume, bring us somewhere near to the outer limit of the crural ring. With the point of a pair of compasses on the point *B* (fig. 3 (I)), an arc *FD* with radius  $3\frac{1}{2}$  cms. has been drawn. This cuts the ilio-pectineal line at the point *D*. From *B* and passing through *D* a straight line *BDE* has been drawn. The angle *ABE* is the required inguino-pectineal angle, and can be accurately measured with a protractor. It is not claimed by me that this method is devoid of fallacy, and of course no account has been taken of the slight curvature of Poupart's ligament. The projected angle may not accurately represent the true inguino-pectineal angle, but I do maintain that even if the figures are not absolutely correct, they are of value for purposes of comparison of the two sexes. At all events the method is much more accurate than an attempt to measure the angle direct in the post-mortem room.

*Method II.* (*Measurement of the inguino-pubic angle.*) After having thus estimated this angle from 12 male and 12 female ossa innominata (only bones with undoubted sexual characteristics were used), I discovered another, easier, and (so it seemed to me) rather more accurate method of obtaining a slightly different but yet similar angle.

In this second method (which I afterwards used with the same male and female ossa innominata), the only real difference is the way in which the bone is placed on the paper. The bone is held with the acetabulum facing downwards and the posterior half of the iliac crest facing upwards (see Plate I, fig. 2). If the bone has been a right-sided one, I have, for convenience in projecting, usually placed the pubic spine away from, and the anterior superior iliac spine towards, myself: if a left bone has been used, *vice versa*. I describe this method as more accurate as both the spines referred to lie actually on the paper, whereas in

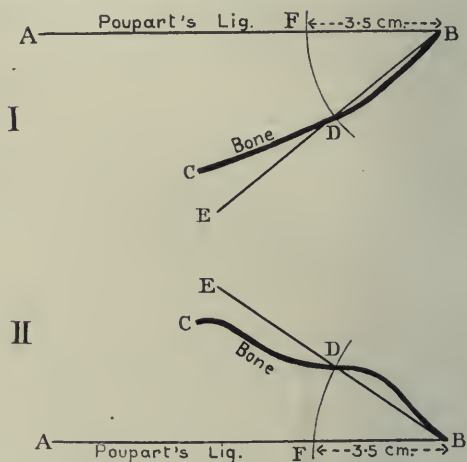


Fig. 3. The projected Inguino-pectineal and Inguino-pubic angles showing how to measure them.

- I. Inguino-pectineal angle—right side (female).
- II. Inguino-pubic angle—right side (male).

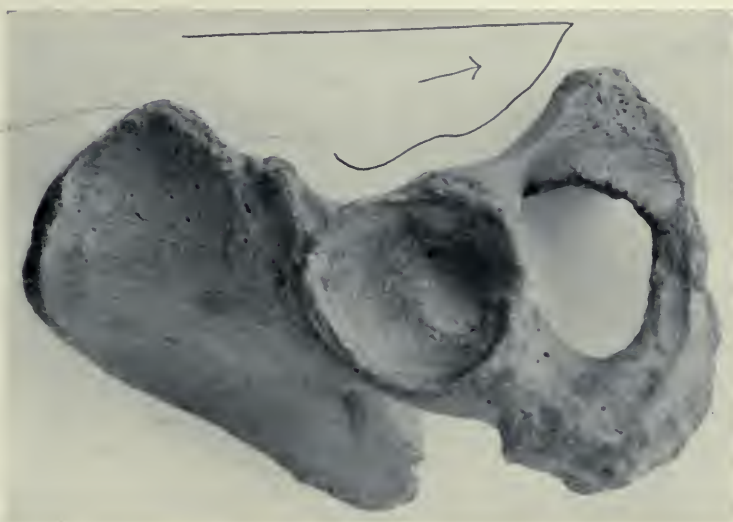


Fig. 1. To show the position of the innominate bone used in projecting the inguino-pectineal angle. The observer is looking directly down from above. The arrow points into the (projected) angle. The bone has been moved slightly towards the observer after projecting in order to make the result clearer.

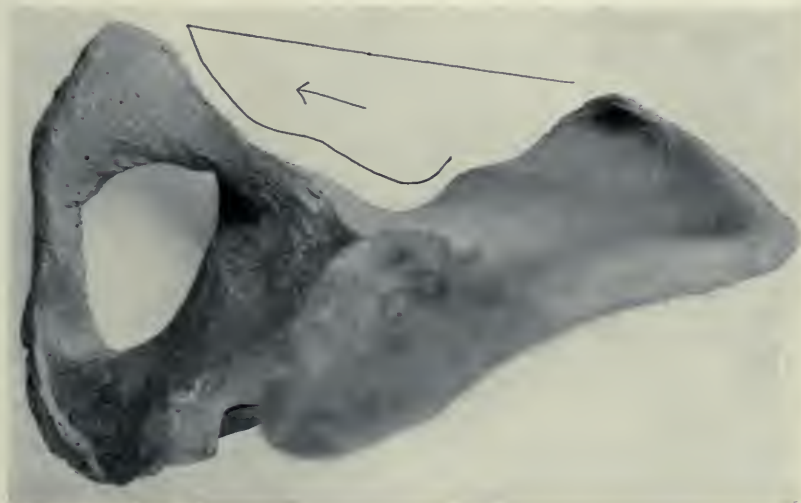


Fig. 2. To show the position of the innominate bone used in projecting the inguino-pubic angle. The observer is looking directly down from above. The arrow points into the (projected) angle. The bone has been moved slightly after projecting in order to make the result clearer. In carrying out the projection the specimen would be so placed that the arrow pointed directly away from the observer.





Method I. roughly an inch separated each from the paper. It therefore becomes easier to project these points (see fig. 3 (II) *A* and *B*) on to the paper. In running the pencil from the pubic spine for 3 inches or so towards the iliac spine, it will be seen that one is no longer projecting the ilio-pectineal line, but rather the anterior border of the pubic ramus. For this reason I describe the angle obtained as the inguino-pubic angle (see fig. 3 (II)).

The anterior border of the pubic ramus lies almost on the paper in projecting. It has seemed to me, that since the anterior border of this portion of bone forms a more direct boundary of the pelvo-crural interval (communication between abdomen and leg) than does its posterior border (the ilio-pectineal line) the inguino-pubic angle concerns us more than the inguino-pectineal. In fig. 3 (II), the lettering has been made exactly similar to (I), and the result having been obtained by the same method no further explanation is necessary.

### Results.

*Method I.* Estimation of *inguino-pectineal angle* of 12 male and 12 female innominate bones:

Table I.

Sex	Variation	Average
Male inguino-pectineal angle .	$32\frac{1}{2}^{\circ}$ to $44^{\circ} = 11\frac{1}{2}^{\circ}$	$38^{\circ}$
Female inguino-pectineal angle	$32^{\circ}$ to $43\frac{1}{2}^{\circ} = 11\frac{1}{2}^{\circ}$	$38^{\circ}$

*Method II.* Estimation of the *inguino-pubic angle* of the *same* 12 male and 12 female innominate bones.

Table J.

Sex	Variation	Average
Male inguino-pubic angle .	$21^{\circ}$ to $43^{\circ} = 22^{\circ}$	$34\frac{1}{2}^{\circ}$
Female inguino-pubic angle	$27^{\circ}$ to $43\frac{1}{2}^{\circ} = 16\frac{1}{2}^{\circ}$	$34\frac{1}{3}^{\circ}$

The above figures give a negative result to the enquiry undertaken.

As regards the inguino-pectineal angle a variation of  $11\frac{1}{2}^{\circ}$ , and an average measurement of  $38^{\circ}$  is recorded in each sex. As regards the inguino-pubic angle, that of the female, according to this series, is on the average exactly one quarter of a degree greater than that of the male. This amount is negligible. The variation in the angle measured is, however, considerably greater in the male.

We can assert then that if Poupart's ligament may be considered to be a firm and immovable boundary, there is no definite increase in the size of the female inguino-pubic angle (and hence presumably in the antero-posterior measurement of the female crural ring).

Poupart's ligament is not quite immovable. It is a distinct possibility that the weaker female ligament is more liable to lengthen and slacken than the male, thus permitting a greater susceptibility of the prolapse of abdominal contents into the thigh.

## V. SOME OTHER ANATOMICAL POINTS.

*The angle between the common iliac arteries.* Cunningham's *Text-book of Anatomy* (3rd edition) states that the angle between these two diverging vascular trunks varies, being about  $60^\circ$  in the male and  $68^\circ$  in the female.

This fact is in accordance with what has already been demonstrated concerning the relative narrowness of the female ilio-psoas muscle. These vessels lie upon the inner border of the ilio-psoas above, and internal to that border below. The greater angle between the vessels is very suggestive of a wider crural ring in the female—which the foregoing measurements and arguments have already proved to be actual fact.

*Pelvic obliquity.* The obliquity of the pelvic inlet is stated to make an angle of  $60^\circ$  with the horizon (Frazer(8)). Arthur Thomson (11) makes an unsupported statement that the obliquity is greater in the female.

Quain (12) gives the inclination of the pelvic inlet with the horizontal as varying from  $60^\circ$  to  $65^\circ$ ; Buchanan (13) gives it as varying between  $50^\circ$  and  $60^\circ$ . Neither of these authors suggests any definite sexual variation. Holden (14) gives definite figures for each sex but gives the male obliquity as  $54^\circ$  and the female as  $50^\circ$  which makes the male obliquity greater. And so opinion varies with different authorities. If Thomson's statement is correct, it seems a justifiable suggestion that, a greater female pelvic obliquity may be an important factor in the production of femoral hernia, the weight of abdominal contents thereby being more forwardly directed towards the abdominal wall and the pelvo-crural interval.

*Proportional length of Gimbernat's to Poupart's ligament.* It is to be observed that the average length of Gimbernat's ligament in both sexes is 2 cm., while that of Poupart's ligament varies, being 4 mm. greater in male than in female. The average proportional length of the former to the latter is then:

Males 1 : 6,  
Females 1 : 5.7.

It appears then that in the female Gimbernat's ligament is relatively greater than in the male—contrary to what we should expect seeing femoral hernia is commoner in the female. Gimbernat's ligament cannot then account for the unequal occurrence of this hernia in the two sexes. It can, and probably does, act as one of the determining causes of femoral hernia in cases where it is ill developed (without respect to sex at all). In support of this statement I would quote the following case: In Case 52 of my post-mortem series, a right strangulated femoral hernia was found at autopsy. Poupart's ligament measured 12.7 cm. The right Gimbernat's ligament had been incised to free the hernia; let us assume it was the same size as the opposite and uncut ligament. This measured 1.6 cm. The relation of Gimbernat's to Poupart's ligament is here as 1 is to 7.9. The former ligament was therefore very poorly developed. In the same case the interspinous distance was 4 cm. above the average but that of Poupart's ligament was only 7 mm. above average. It is



interesting to record also in this case that the transverse measurements of both crural rings (? reliable) were larger than those of any other recorded by me. The right (herniated) one was 2.4 cm.: the left (normal) one was 2.0 cm. This large size cannot be set down as due to a poorly developed and narrow ilio-psoas: as a matter of fact that muscle was unusually wide and well developed. The small size and ill-marked character of Gimbernat's ligament must, therefore, be considered as a powerful predisposing cause of the hernia in this case.

The antero-posterior measurement of the lacuna vasculosa (and therefore presumably that of the crural ring) was rather larger (3 mm.) than the average. This suggests an enlarged inguino-pubic angle which is likely to be due to a slackened and enfeebled Poupart's ligament.

### SUMMARY OF PART III.

It will be convenient here to mention briefly the facts already arrived at, with the conclusions which are drawn from them.

1. The female *false* pelvis is either relatively narrower than the male, or else is equal to it: it is certainly not greater. Therefore the "wider pelvis theory" of femoral hernia is untrue.

2. The female Poupart's ligament is relatively shorter than the male. Therefore the pelvo-crural interval is (transversely) narrower in the female. This still further (if need be) disproves the "wider pelvis" explanation of hernia.

3. The female Gimbernat's ligament is relatively larger than its male counterpart in the ratio of 6 to 5.7. Therefore it is not Gimbernat's ligament which is responsible for the greater frequency of female femoral hernia. We must concede, however, that smallness and an ill-developed character of this ligament are predisposing factors in the production of hernia *apart from sex*.

4. The female ilio-psoas muscle is relatively narrower than the male one. Series II gives the relationship of the relative breadth of this muscle in the two sexes as: female is to male, as 1.36 is to 1.43. We conclude that the lesser muscular development of this structure plays a part as a predisposing factor in the etiology of femoral hernia.

5. The female lacuna vasculosa (transversely) is relatively greater than that of the male in the proportion of 5 to 4. Since the femoral vessels are probably, and the ilio-psoas is certainly, narrower in the female, we conclude that the disproportion, between the transverse measurements of the female and male crural rings, is even more pronounced than the ratio expressed above.

6. The antero-posterior measurement of the lacuna vasculosa (and therefore presumably of the crural ring) is given by the figures as larger in the male (? reliable). The inguino-pubic angle (also an indicator of this measurement) is, however, negligibly greater in the female. The conclusion is, that unless Poupart's ligament is more liable to "give" in female than male, this measurement can have no bearing on the production of a hernia.

One is driven to the conclusion that the greater predisposition of the female sex to femoral hernia, is related to the lesser development of the ilio-psoas, which allows the femoral vessels to diverge more than in the male, and so creates a wider crural ring. Probably, Poupart's ligament is weaker, and more prone to stretching in the female. This would account for widening of the inguino-pubic angle, and antero-posterior increase of the crural ring. In men the same predisposing causes are probably at work, but occur less often on account of males being usually better developed than women in the muscular sense, and on account of a stronger Poupart's ligament.

Ill-development of Gimbernat's ligament may be a causative factor in both sexes.

#### Part IV

##### FACTORS ARISING OUT OF DEVELOPMENTAL PROCESSES

Can the crural canal be of any embryological significance? This question loomed large before me when, on examination of Case 7 of my post-mortem series, I found the following somewhat remarkable state of affairs:

The subject was a male, 59 years of age, who had died of heart failure due to coronary arteriosclerosis. I discovered a peculiar bilateral "cyst" closely applied to the inner border of each ilio-psoas muscle. It was elongated in shape, and about  $\frac{3}{4}$  in. wide. It was retroperitoneal, and the peritoneum was easily stripped off from it. It extended upwards about  $1\frac{1}{2}$  ins. above Poupart's ligament on either side, and when incised a small amount of thick white or yellow "ropy" fluid escaped. This did not appear to be pus. A finger inserted through the incision showed that each "cyst" was lined by a smooth membrane, and the finger passed freely down beneath Poupart's ligament for about 3 ins. into the leg towards the small trochanter. No external "tumour" was visible. This peculiar cyst was not beneath the ilio-psoas fascia: it abutted against the concave edge of Gimbernat's ligament, which was poorly developed on both sides, measuring only 1.1 cm. (The length of Gimbernat's ligament was to that of Poupart's in this case as 1 is to 11.)

My first suggestion regarding this case was that it might be a double encysted hydrocele of the crural canal (comparable to a hydrocele of the canal of Nuck in the female), and might have arisen by a cutting-off from the general peritoneal cavity of a peritoneal diverticulum into the thigh. Such a thought presented to me the interesting possibility of a "processus cruralis" of peritoneum descending into the leg, and occurring normally at some stage of development in every individual. If such were really the case then femoral hernia would no doubt be due to the abnormal non-obliteration of a normal processus cruralis.

This view, however, seems untenable, since:

1. A condition similar to that described, has, as far as I know, not been described before. Were such a peritoneal diverticulum normally present in

every individual at some stage, cases of hydrocele of the (crural) canal would not be rarities.

2. The embryological use of such a diverticulum cannot be imagined.
3. A firm connection between cyst and peritoneum would be expected if one were derived from the other. None was found.
4. The upper end of the "cyst" was not *at* the upper end of the crural canal.
5. Thick "ropy" fluid is not usually found in hydroceles.
6. Since Gimbernat's ligament was so ill-developed, a hernia would have been expected in this case, if, at any stage, a diverticulum communicating with the peritoneum had been present.

What the condition seen actually was, I am unable to say. Considered impartially, however, it does not appear to throw any light on femoral hernia.

R. W. Murray (15) has brought forward remarkable evidence in favour of the saccular theory of hernia. Although femoral hernia is said to be uncommon in children, he has collected definite evidence, in the writings of others, of at least 104 cases which occurred in children under 15 years of age (52 of which first appeared before 10 years of age). Again, in examining 200 consecutive bodies post-mortem, he found 47 of them presented peritoneal diverticula (femoral, inguinal and umbilical) some of which were bilateral, so that 68 diverticula in all were found in 47 subjects. Amazing as it may seem, as large a number as 52 out of the 68 protrusions were femoral diverticula, and were therefore potential femoral hernia sacs. As Murray points out, none of these subjects had ever had any signs or symptoms of hernia during life. He therefore concludes that potential femoral hernia sacs are found in certain persons throughout life, which may or may not give rise to actual hernia. Such "preformed" sacs in the femoral region do not usually give rise to hernia in children, but did do so in the 104 cases quoted. Strong evidence of the truth of this preformed saccular theory is found in a case recorded by Owen (30). A girl of six years of age who previously had had no hernia, *suddenly* developed a strangulated femoral hernia. Obviously the peritoneum could not be distended suddenly. The sac must have been waiting for any abdominal content which might enter. Murray states that these preformed femoral sacs owe their origin to abnormally attached auxiliary bands of the gubernaculum, dragging on the peritoneum in the vicinity of the crural ring, and so bringing it down into the thigh. Fergusson (16) relates a case which gives distinct colour to this proposition. He records a cruro-scrotal hernia which left the abdomen by the crural ring and yet found its way into the scrotum. The spermatic cord was found in the crural canal, and the inguinal canal was absent.

Murray (15) has looked for gubernaculum tissue (histologically) in the neighbourhood of the fundus of femoral hernia sacs obtained by operation. In one obtained from a male subject, he found small bundles of faintly striated muscle which he avers to be gubernacular remains.

In the latter part of my post-mortem series and where it was possible



owing to the peritoneum in the lower part of the abdomen having been left *in situ*, I made a search for peritoneal diverticula. 15 cases were examined thus (6 male and 9 female). As shown in the table below 6 of these 15 subjects (including 3 of each sex) together presented 9 preformed hernial sacs. Eight of these were inguinal, and one only was femoral:

Table K. *Potential hernial sacs found in 15 subjects examined: 6 subjects were male, 9 were female.*

Case No.	Sex	Age	Potential or preformed hernial sac found.
35	Male	46	Right inguinal (3 ins. long).
43	Male	38	Left inguinal (large orifice).
44	Male	59	Left inguinal (sac large, orifice 2 mm. wide).
56	Female	35	Right and left inguinal (wide orifices).
53	Female	40	Left femoral.
51	Female	70	Two right inguinal (one direct, one indirect). Left inguinal (indirect).

Two of the above cases gave such clear evidence of preformed (and of course empty) sacs that I removed them after the post-mortem examination with certain pelvic viscera, and had them photographed. Plate II, figs. 1 and 2 show the specimen of a left preformed femoral sac obtained from a woman of 40 years. On the left side the mouth of the sac is seen with a small vegetation-like piece of tissue proceeding out of it. This appeared to be a piece of omentum which, having obtained a new attachment inside the sac, had now lost its former attachment. From mouth to fundus this sac was 5.6 cm. long. On the right is seen a depression or "pucker" of peritoneum over the site of the crural ring. There is no true sac on this side—what appears to be sac on the reverse of the same specimen (Plate II, fig. 2) is only a thickened aggregation of extra-peritoneal fat with a lymph gland inside it. The uterus was pushed back in order to display the specimen. Bladder, round and ovarian ligaments, ovaries, and Fallopian tubes also appear on the photograph. The "depression" of peritoneum on the right side could be evaginated down the crural canal by the finger for about  $\frac{1}{2}$  in. I have observed this "baggy" condition of the peritoneum over the crural ring in at least four other subjects where no sac was present. In Plate II, fig. 1 the thickening of peritoneum which occurs on the pubic side of the neck of the sac is well seen. According to Murray this thickening is always present, and may be made use of in operating in order to know when one has dissected back as far as the neck of the sac.

It appears then that the presence of preformed hernial sacs, of apparently indiscriminate distribution, is an undoubted fact.

Femoral hernia sacs, and also these unsuspected preformed femoral sacs discovered only at autopsy, are found usually between Gimbernat's ligament and the femoral vein.

Macready (17) has put on record a case in which he found three femoral sacs on one side in one and the same subject, a woman between 40 and 50 years of age. One of these was the normal femoral sac and had its neck just internal

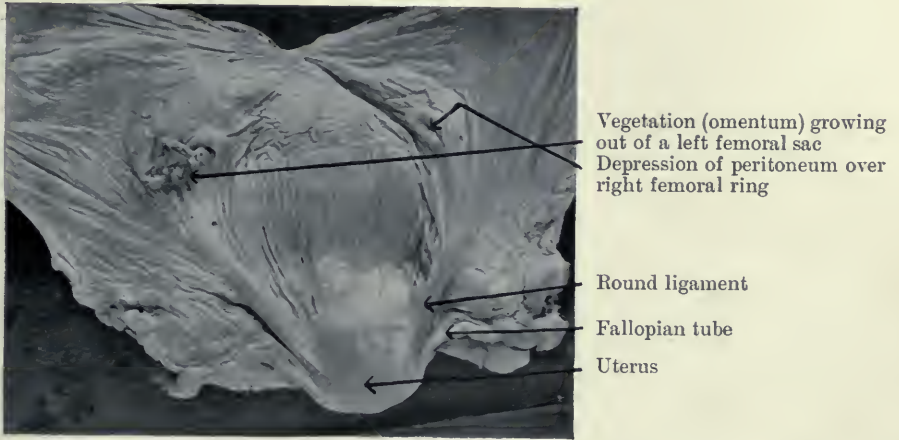


Fig. 1. Specimen from a female subject showing a left preformed femoral sac (peritoneal aspect).

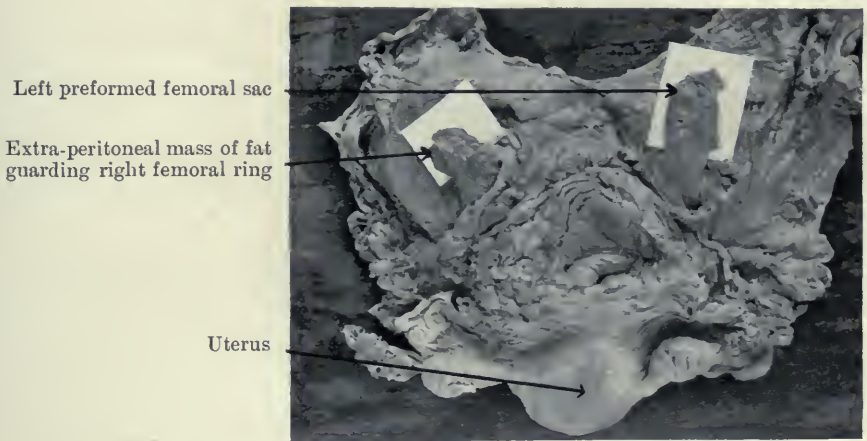


Fig. 2. Same specimen as above (non-peritoneal aspect).





to the femoral vein. The second lay partly in front and partly to the outer side of the femoral vessels. The neck of the third passed through a small opening actually in Gimbernat's ligament, near to the pubic spine. The prevascular femoral sac has also been found by others either at operation or autopsy. Partridge (18), Fabricius (19), Zinner (20), and A. V. Moschcowitz (21) all speak of having met with this type of sac. Teale (22) mentions that Stanley twice found a prevascular femoral hernia at post-mortem examinations. Finally Narath (23) records six cases of prevascular femoral hernia, which, strange to say, succeeded the reduction of a congenitally dislocated hip-joint in each instance.

The fact of three femoral sacs co-existing on one side in one patient, as Macready describes, seems in itself powerful evidence that the sacs had arisen by some developmental anomaly.

Spencer and Gask (24), writing in 1910, state that it is general belief that femoral hernia takes its origin in a pouch of peritoneum carried down into the leg in the course of development of the vessels. On the contrary, however, no peritoneal pouch can be constantly found. There is no reason to suppose that the femoral vessels, which must "develop" in every case, should carry a diverticulum down in some and not in others. It is, of course, possible that a peritoneal diverticulum may be carried down in *every* case by the developing femoral vessels, and that the sac so formed normally undergoes a process of obliteration. In spite of this possibility, the explanation of the origin of a femoral hernia sac given by Spencer and Gask, entirely fails to account for Macready's three sacs in one thigh. Murray's suggestion that femoral hernia originates in sacs dragged down by excessively developed bands of gubernaculum which are normally present though feeble and slender, is a much more feasible theory. This theory will account for Macready's three sacs, it being quite simple to imagine very occasional abnormal bands of gubernaculum which have attachment to peritoneum in front of or external to the femoral vessels, and (possibly) secondary attachments to the superficial fascia of the thigh below. Besides which, Murray has demonstrated faintly striated muscular fibres in the fundus of a femoral sac. This he has been able to do, however, in one case only. In other cases he has failed.

I have myself examined histologically the tissues found at the fundus of four femoral hernia sacs (three obtained at operation, and one at autopsy). Two were from males and two from females. In no instance could I, even after careful and prolonged examination of the sections, find any tissue which I could unhesitatingly say was striped muscle and which might therefore be of gubernacular origin.

While holding to the opinion therefore that the sac of a femoral hernia is in every case a congenitally preformed sac, and that the causative agent in the formation of such a sac is probably the gubernaculum, I consider that further search for gubernacular tissue is necessary before the latter point can be definitely cleared up.

*The Femoral Sheath.* Upon first acquaintance the femoral sheath and especially its "innermost compartment" are always a profound mystery to beginners in anatomy. This is not to be wondered at, since neither of these structures exists in the dissecting room as described in anatomy books. The descriptions there found have come originally from the surgeon who, in well marked cases of femoral hernia sees various layers and definite compartments of a sleeve of fascia closing on the femoral vessels. Surgery is a very good friend to anatomy, but an equally bad master. In order to investigate the structure of the so-called femoral sheath, I obtained a fresh foetus, and cut out three blocks of tissue including skin and underlying structures, without in any way disturbing the parts by dissection. The three blocks of tissue were planned in each case to include the external iliac or femoral vessels.

Block A was taken about  $\frac{3}{4}$  in. above *Poupart's ligament*. Block B was taken at the level of *Poupart's ligament*. Block C was taken from the thigh below the level of the femoral sheath.

A is then above, B is at the level of, and C is below the femoral sheath.

In the first of these sections the vessels fell away in the process of preparation: in the other two they remained *in situ*. The tissues were fixed in 10 per cent. formol and sections stained by two methods: (1) haematoxylin and eosin; (2) haematoxylin and van Gieson's stain.

In the sections of B and C no distinct layers of a femoral sheath are seen. What is seen is a mass of undifferentiated connective tissue between and around the femoral vessels and anterior crural nerve. This passes imperceptibly from the adventitia of the vessels (or the inter-fascicular connective tissue of the nerve) on the one hand, to the various aponeurotic fasciae in the neighbourhood on the other hand.

Plates III, figs. 1 and 2 are microphotographs of the section from Block C, i.e., they represent a level below the so-called femoral sheath. In this situation, however, a sheath is formed for the vessels by the undifferentiated connective tissue belonging to all the surrounding structures. This "sheath" (in a position where none has been described) is in my sections much better defined than is the "sheath" at the level of *Poupart's ligament* (where a "femoral sheath" is *still* described).

Wherever structures lie together in the body (and especially nerves or vessels) the surrounding connective tissue, often of a more or less dense nature, ensheathes them and incorporates them into one matrix.

The external iliac vessels in leaving the abdomen are adherent to the ilio-psoas and transversalis fasciae. These strata fuse with the adventitia of the vessels at the point of exit. Because, first of all, surgeons found femoral hernia sacs surrounded by somewhat dense connective tissue continuous with that round the femoral vessels, and secondly, in a few cases anatomists have by tedious and artificial dissections, been able to demonstrate "compartments" in this region, the exceedingly delightful idea of a femoral sheath was originally conceived. One of the main uses of such a conception was that, coming from

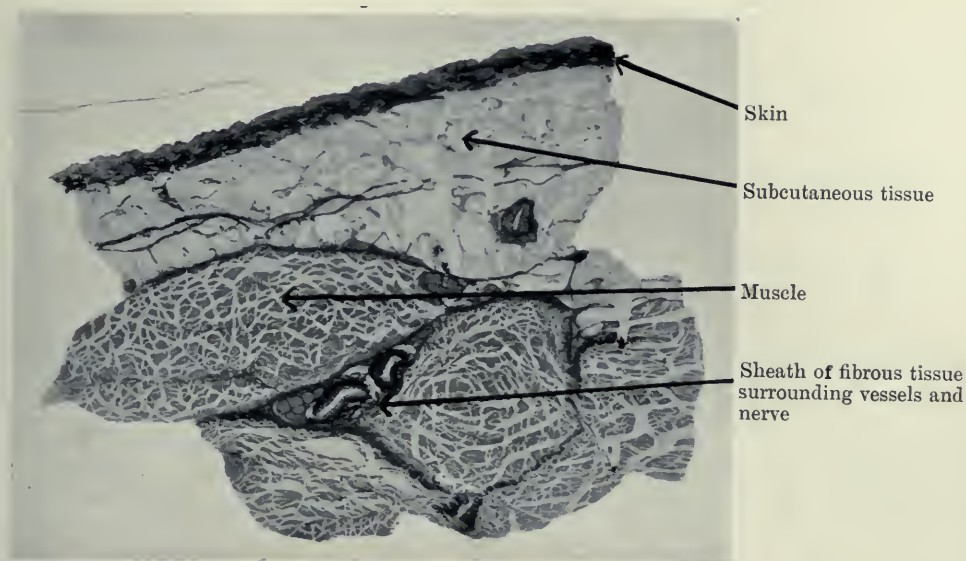


Fig. 1. Microphotograph of a transverse section of the femoral vessels and adjacent parts below the (so-called) femoral sheath.

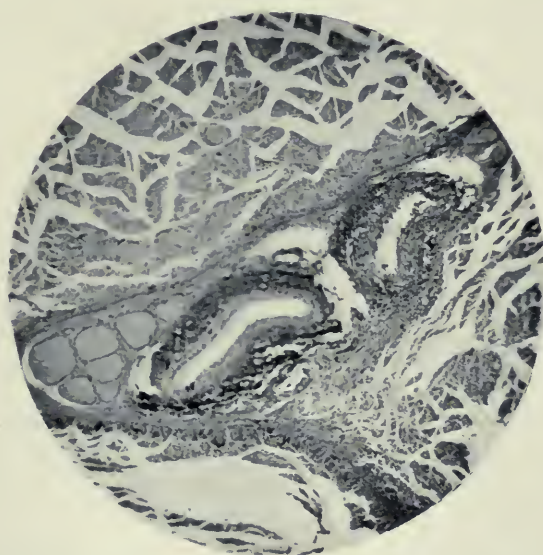


Fig. 2. Enlargement of part of same specimen as above. To show mass of fibrous tissue around femoral vessels.





the surgeon, it fitted in with the surgical findings in femoral hernia and it explained anatomically a weak spot in the abdominal parietes, namely, a funnel with an upper end open to the abdomen (crural ring and canal).

But we ~~now no~~ longer believe that abdominal contents carry parietal peritoneum before them into the leg. We have a new conception of femoral hernia—that it can only occur where a preformed sac (or peritoneal funnel) awaits it; in other words that, although there may be other predisposing causes of femoral hernia, the *determining cause* is a preformed sac.

Why should we carry on the farce of keeping up the old inaccurate anatomical descriptions, especially when such descriptions are not even necessary to explain pathological processes? The time has come to do away with such things. Around the femoral artery and vein is a mass of undifferentiated connective tissue. The combined ilio-psoas and transversalis fasciae are pierced by these vessels *at the level of Poupart's ligament. At the same level* (not an inch and a half lower down as the books say) these fascial layers fuse with the perivascular tissue. The increased thickness and density of the perivascular tissue formed by this fusion gives rise to what we have for so long named the “femoral sheath.”

The crural ring is the interval (probably notable by its absence in the normal living subject) between Gimbernat's ligament and the femoral vein.

The crural canal consists of that part of a preformed femoral sac which descends from the position of the crural ring. *It does not exist* (not even potentially) unless a preformed femoral hernia sac is present.

## Part V

### FACTORS ARISING OUT OF PHYSIOLOGICAL AND PATHOLOGICAL PROCESSES

The main facts arrived at concerning femoral hernia are that its determining cause is a preformed femoral sac, and that its greater frequency in women is due to a lesser developed ilio-psoas muscle which acts as a predisposing cause.

Granted the presence of a sac, contributory factors may be any cause of:

- (1) Increased abdominal pressure (increased “push” from behind).
- (2) Decreased resistance in the vicinity of the crural ring (decreased “counter-push” in front).

In the records of 100 cases of femoral hernia operated upon at the Manchester Royal Infirmary which I analysed, 81 cases were females, and 19 cases were males.

Out of 57 of these women, 40 were married and 17 were single. It appears from this that femoral hernia is rather more than twice as common in married as in single women, which at once suggests pregnancy as a factor in the etiology of femoral hernia. In pregnancy, abdominal pressure increases as the gravid uterus rises and enlarges. In the later stages the hernial orifices are somewhat protected by the uterus itself. But at the same time the abdominal wall has

to bear the extra brunt of supporting a heavy uterus over some months of time. During that period the muscles are stretched and enfeebled, and the lower abdominal wall tends to "sag" downwards and forwards, which also causes Poupart's ligament to "sag": hence the inguino-pubic angle is enlarged and when pregnancy is over, the crural ring has a bigger mouth (antero-posteriorly). Labour may be a time of special danger from the point of view of femoral hernia, because during that period intra-abdominal pressure is great (bearing down), and as the uterus empties, the abdominal organs have new access to (possibly) enlarged femoral rings, guarded by exhausted and attenuated tissues. Dollar (25) mentions the fact that Dandrieux saw a cow develop crural hernia during labour. This is an interesting fact, the more so as femoral hernia is excessively rare in animals.

The ninth case in my series was a woman who had a strangulated femoral hernia, due presumably to the increased abdominal tension of a three months' pregnancy which autopsy revealed.

In the records of femoral hernia cases which I searched through, I was able in 7 male and 19 female cases to find some alleged cause for the hernia, suggested either by the patient, or perhaps in some cases by the house-surgeon after a close cross-examination of the patient. These alleged causes of femoral hernia I have set down below, each with the number of cases for which it was alleged to be responsible.

Table L.

Alleged cause of femoral hernia	Females	Males
*Chronic constipation ... ..	2 cases	1 case
*Bronchitis or chest trouble ... ..	4 cases	2 cases
*Movable kidney ... ..	1 case	—
*Occurring soon after confinement ...	3 cases	—
Prolapsed uterus since last confinement	1 case	—
Doing "washing" near end of pregnancy	1 case	—
Sudden strain ... ..	4 cases	—
Heavy lifting ... ..	1 case	1 case
Heavy work ... ..	2 cases	—
Accident ... ..	—	1 case
Associated inguinal hernia ... ..	—	2 cases
Total ...	19 females	7 males

\* Cause related to loss of muscular tone.

Let us first of all consider the case of women only. The type of woman who frequently comes with any form of hernia is well known—a large fat woman, with a somewhat pendulous abdominal wall; a shapeless subject who seems to have replaced muscle by fat. She has in many cases had a number of children, leaving her with a flabby abdominal wall. She is more often than not the subject of chronic constipation. The viscera in general may have "fallen."

Lockwood (26) has with great labour recorded the length and height of various mesenteries and the excursion of the intestines in 100 subjects without herniae, on account of his firm conviction that elongation of these peritoneal



folds played a large part in the etiology of hernia. We do not pay much attention to these facts now, as it has been proved that the normal mesentery is quite long enough to allow the bowel to pass beyond the inguinal and femoral rings. There is, however, much valuable information to be derived from Lockwood's observations. It is not visceroptosis itself which plays so large a part in hernia; but the condition which is so frequently responsible for visceroptosis is, to my mind, all-important. That condition is *loss of muscular tone*—and is often coupled with lack of muscular development.

Now let us look at the table again. The first four alleged causes given are related in some way to lack of muscle-tone, for chronic bronchitis is a cause of this condition; movable kidney and frequently chronic constipation are effects of it. Repeated pregnancies weaken the musculature and decrease their tone—hence the increased “shapelessness” of the multiparous.

A prolapsed uterus may be evidence of tonelessness of muscle. It therefore appears that out of 19 females with femoral hernia, 10 and possibly 11 cases present signs or symptoms of loss of tone of the musculature. The other nine cases are more related to increased abdominal pressure, but for aught we know may also have shown loss of tone.

In the seven male cases where alleged causes for the hernia were found, three are due to conditions likely to be related to loss of tone. The association of inguinal with femoral hernia seems to me to indicate the same condition, but as my contention here is to show a likely relationship between loss of tonicity of muscles and hernia, this may scarcely be admitted as part of the argument.

An analysis of the 100 cases of femoral hernia with regard to age incidence is given below. Unfortunately it has not been possible to find out the age of onset of these herniae, so age at operation has had to be made use of instead. Since the age incidence is given in decades it is probable that only slight inaccuracy has arisen from this fact.

Table M. *Age Incidence of Femoral Hernia in 100 cases.*

Years of age	Female cases	Male cases
10-20	1	1
20-30	14	3
30-40	22	4
40-50	17	5
50-60	15	5
60-70	10	1
70-80	2	0
Total	81	19

From this analysis it appears that femoral hernia is most apt to occur between 30 and 40 in women and between 40 and 60 in men. Why the difference in the sexes? Let us consider for a moment the ages in either sex at which, under ordinary circumstances, lack of muscle tone is likely to have reached its maximum. In men this time is likely to occur after middle life, for men as

a whole are of good muscular development and it is only in later life that muscular tone is in any way impaired. Even then the diminution is apt to be slight, and relative only to the heavy work which many of them carry on. In women pregnancy plays a large part in reducing the tone of muscles, and hence it is in the prime of life (30–40 years) and well before the menopause, that women are most prone to femoral hernia.

Added to this there is the fact that some women practise "tight lacing" which is apt to induce loss of muscular tonicity. Again, women as a whole are less well muscularly developed than men, and a certain number of them (in the leisured classes especially) live indolent lives, such as are apt to allow impairment of muscular tone with the supervention of a condition of "flabbiness."

It follows that women as a class are of poorer muscular development and on account of pregnancy, labour, massive gynaecological tumours (to which they are so liable); and the living of a less muscular life than men, they are apt to become the subjects of reduced muscular tone more easily and at an earlier age.

By contrast, men are of greater muscular development, and on account of the harder lives they lead, muscular development is increased and muscular tone in most cases maintained till a later period of life. It is likely that in a small number of male cases muscle tone becomes impaired earlier than usual, in which case it will be reasonable to suppose that lack of muscular tone plays a part in the production of a large percentage of all ruptures without distinction of sex.

Why should femoral hernia be so rare in children? Bull and Coley (27) speak of a series of 1381 femoral herniae out of which only 18 occurred under the age of fourteen years. Muscular tone is on the upgrade until early adult life in any case. Children are not usually indolent: on the contrary, they are very active. The pelvis of the child is narrow. Moreover the angle of iliac divarication (Cleland (9)) is diminishing during adolescence, and until early adult life. The pelvo-crural interval is therefore also decreasing in transverse length. Incidentally children do not undertake heavy work, nor are they exposed to "sudden strain," which is notorious as an exciting cause of hernia—at least among patients.

When the large part which deficient muscle tone seemed to have in femoral hernia first occurred to me, I had hoped to X-ray a number of femoral hernia patients after a bismuth meal, in order to examine their gastro-intestinal muscle-tone. This I have been unable to do as yet.

I feel convinced, however, that such examinations if made, together with the examination of the condition of the abdominal musculature of femoral hernia patients, either before or during operation, would emphasize the importance which I have insisted on, of decreased muscle-tone and development, as a significant factor in the etiology of femoral hernia.

GENERAL SUMMARY OF THE FACTORS CONCERNED  
IN THE ETIOLOGY OF FEMORAL HERNIA

1. Man suffers from a general anatomical predisposition to femoral hernia, on account of weakening structural alterations in his groin, following on the adaptation to the plantigrade posture and mode of progression.

2. The occurrence of femoral hernia *depends* on the existence of a pre-formed femoral diverticulum of peritoneum brought down (probably) by gubernacular bands of abnormal attachment or development. Such sacs frequently exist and Murray's table does not suggest any marked unequal sexual distribution of them.

3. Granted the presence of a preformed sac, the condition of muscular tone and development is an important determining factor. It is because women are naturally of comparatively inferior muscular development (e.g. relative narrowness of ilio-psoas), and are liable to many conditions (especially pregnancy) destructive to muscle-tone, and from which men are free, that so marked a disproportion of sex incidence in femoral hernia occurs.

4. Women are subject to wide ranges of change of intra-abdominal pressure, and yet comparatively have less muscle-power and tone to guard their abdominal parietes. Men are little subject to changes of intra-abdominal pressure, and even should increase of the latter occur, they are more able to guard their abdominal parietes on account of better muscular development and a relatively more perfect muscle-tonus.

5. Poor development of Gimbernat's ligament may in either sex be a factor, although normally the female ligament is relatively longer than that of the male.

6. It is possible that pelvic obliquity plays a part. The female pelvis is, by some, said to be more oblique than the male pelvis.

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## A CASE OF CONGENITAL SCOLIOSIS DUE TO THE SUPPRESSION OF HALF A VERTEBRA

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CONGENITAL scoliosis is a rare condition and very little attention had been paid to this and other congenital malformations of the skeleton until the discovery of the X-rays. A few specimens of this deformity, however, have been preserved in museums.

According to Whitman (1) congenital scoliosis may occur in infants otherwise normal and due apparently to a constrained attitude before birth. It is usually associated, however, with cervical ribs, elevation of the scapula, etc., which conditions can hardly be explained on the ground of posture alone. The deformity may be apparent at birth or it may not be observed until later years when examination by the X-rays shows supernumerary, deficient or fused vertebrae.

The following is a short description of the case: John H. first came under observation at the age of six years; he had a well-marked scoliosis with the convexity to the left in the lower dorsal region; he had compensatory curves above and below. His mother stated that his back had never been straight but she had not sought advice about it as his bowels had always been a constant source of trouble. Ever since birth the child required castor oil to obtain a motion. He was a typical case of congenital idiopathic dilatation of the colon and had been admitted to King's College Hospital on several occasions because of chronic obstruction in the colon. Skiagraphic examinations with opaque meals and enemas demonstrated a very dilated sigmoid colon and rectum, the sigmoid taking up almost the whole of the abdominal cavity. Repeated X-ray examinations of the spinal column clearly revealed a wedge-shaped half vertebra in the region of the eleventh thoracic vertebra on the left side. There were only eleven ribs on the right side while on the left twelve were present, the eleventh articulating with the half vertebra (see drawing reconstructed from skiagram).

This case seems to be one of suppression of the right half of the body of the eleventh thoracic vertebra along with the eleventh rib on the right side. This deformity must arise very early in intra-uterine life and is no doubt due to an error in segmentation.

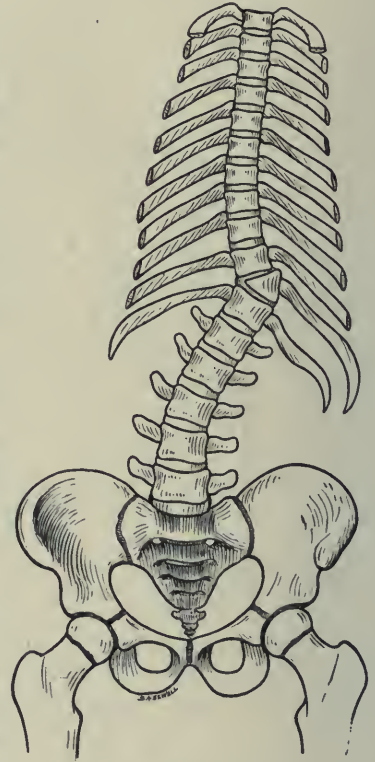
Fitzwilliams (2), in a somewhat similar case in 1908, was inclined to consider that the bone was "atavistic" and due to a persistent hypochordal cartilage.

Fleury (3), in his Parisian thesis for the M.D., gives an account of a case of congenital scoliosis, with a skiagram of the spine; he considered the condition was due to a supernumerary vertebra between the eleventh and twelfth dorsal vertebrae. A year later Mouchet and Broca (4) pointed out that in Fleury's case the scoliosis was due to the suppression of the left side of the body of the twelfth dorsal vertebra and of the twelfth left rib.

Rokitansky (5) as long ago as 1844 found four supernumerary half vertebrae in the spine of a woman aged 46 years. Unfortunately complete details with regard to the number of vertebrae and ribs were not stated.

Mouchet (6) records the case in a girl aged two years where a skiagram showed a supernumerary wedge-shaped imperfect vertebra on the left side between the first and second lumbar vertebrae. Twelve ribs were present on each side which articulated normally with twelve thoracic vertebrae.

It is interesting to note in this case the association of congenital idiopathic dilatation of the colon with the defect in the osseous system. It is a well-known fact that congenital defects of the central nervous system are frequently associated with deformation of the skeletal system and possibly the dilatation of the colon may have been related to some imperfection in the development of that part of the spinal cord associated with the origin of the splanchnic nerves which are given off at the level of the half-vertebra.



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# DEFECTIVE DEVELOPMENT OF THE MANDIBULAR ARCH

## THE ETIOLOGY OF ARRESTED DEVELOPMENT AND AN INQUIRY INTO THE QUESTION OF THE INHERITANCE OF CONGENITAL DEFECTS

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THE literature of that section of Teratology which comprises the deformities resulting from an arrest of development is very voluminous; and until quite recently few attempts have been made to explain either the mode of their production or their bearing on normal developmental processes. It is with the object of throwing further light on the factors concerned in the normal development of the face and the bearing these factors have on the more common defects which come under the notice of the surgeon that the authors have undertaken the study of this type of deformity. Recently Baldwin, Hertwig, Lewis, Mall, McClendon, Spemann, Stockard and others have placed the study of teratology on a more scientific basis than it has been hitherto. These writers have experimented on early fish and amphibian embryos by the use of X-rays, ultra-violet rays, radium emanations and electric currents. Further, the growth of larvae has been modified by alterations in the nature of the fluid in which the embryos have been reared and notably by the use of various chemical reagents, such as the salts of lithium and magnesium and extracts of certain of the ductless glands.

As most of these experiments have been carried out on embryos of anamniota, they prove conclusively that many of the resulting deformities which, when they occur in amniota, have often been attributed to the pressure of amniotic bands, or pressure arising from deficiency of the amniotic fluid, cannot be produced by such factors when they occur in fishes and amphibia, since no amnion is present in these animals; and it seems reasonable to suppose that the same factors which give rise to defects in development such as "Cyclops" or "Brachygnathia" in the anamniota will bring about similar results in the amniota.

In the placentalia the toxic material may be presumed to circulate in the blood vessels of the placenta and thus act injuriously on the developing embryos, preventing union of parts and causing imperfections in growth, or complete arrests of development.

Further, since many of these deformities can, in a certain sense, be produced at will by the experimenter, the factor of heredity is largely, although not entirely, excluded, since defective nutrition of the embryos, which may result in defective development, is often associated with inherited disease. A disease contracted by a grandparent, which has caused a defect of development in one of the parents may be inherited by their offspring, but it is doubtful whether the defect, if it should appear in any of the offspring of the second generation namely the grand-children, is directly inherited. Its appearance in the grand-children may be explained by defective nutrition or malnutrition of the developing embryo which is due to impaired health or to inherited disease present in the mother, e.g. syphilis. In other words, an indirect inheritance, or the inheritance of a secondary effect of disease.

A form of brachygnathia affecting both jaws, is seen in the peculiar little Pekingese dogs, and in the pug. This is a variation which has most probably been established by artificial selection. The condition like brachydactylism or the brachymelism of a dachshund is obviously inherited, and it is an interesting question whether these shortenings of parts should be attributed to germinal variations or to defective developments originally produced by some external cause or some disease affecting the nutrition of the embryos, e.g. in the latter case the presence of rickets in the parent animals may secondarily affect their offspring. The characteristic shortness of muzzle of the Abacus type of the Pekingese dog is so marked that in the ideal form the tip of the nose and the forehead are so nearly in the same plane and the eyes are so far apart, that a silver dollar lying flat on the plane of the dog's nostrils will touch the forehead and at the same time will occupy the interval between, but not cover any part of, the eyes. The name abacus is given to this variety because the form of the dog's head resembles a ball of the Chinese counting board or abacus. The shape of one of these abacus balls may be reproduced by cutting off about one-fourth of its width, from the opposite sides of a wooden sphere, and it is this flattening of the mouth and dome-like crown of the head which is so much admired by the Chinese.

Before describing the varieties of mal-development of the mandibular region in detail, we shall give a brief account of a specimen which represents the least degree of the deformity. It consists of a mere shortening of the lower jaw or brachygnathia, and forms one end of a graduated series of the defect which culminates at the other end in complete absence of the mandibular arch, *Agnathia*, or *Hypoagnathia*.

This specimen is the head of a male lamb which was killed on the fifth day after its birth in accordance with the usual custom of the farmers when a lamb is affected with this deformity and is thereby unable to suckle, and graze. The condition is fairly common, and lambs born with the defect are called by the shepherds hog-jawed sheep (see fig. 1). The lower jaw is imperfectly developed and falls short of the normal by about an inch; it thus comes under the class of brachygnathia. Two incisor teeth have erupted,

the first and third. On turning back the skin and exposing the skull (fig. 2) the maxillary portion of the face appeared normally developed. The lower jaw, tongue and floor of the mouth, except for their small size, appeared normal as were the cartilages of the thyroid and hyoid arches. On splitting open the alveoli it was seen that the second and fourth incisors were present but un-

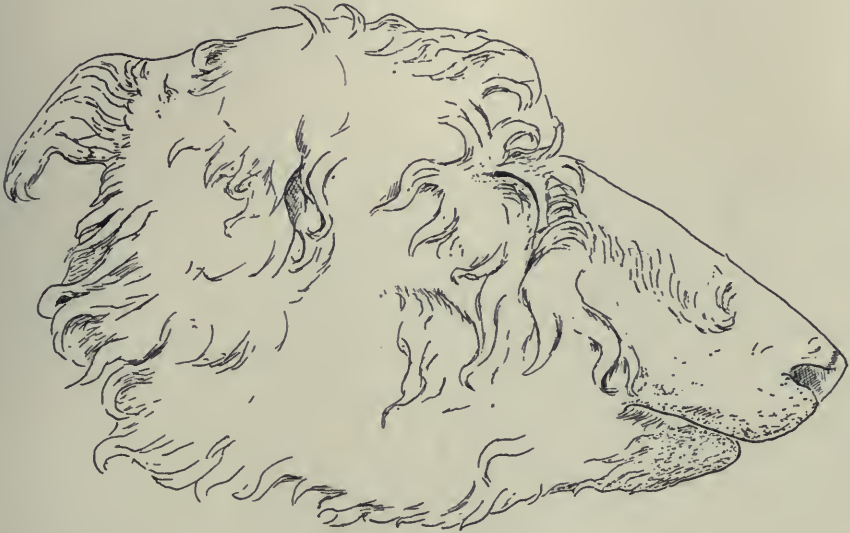


Fig. 1. A "hog-jawed" sheep.

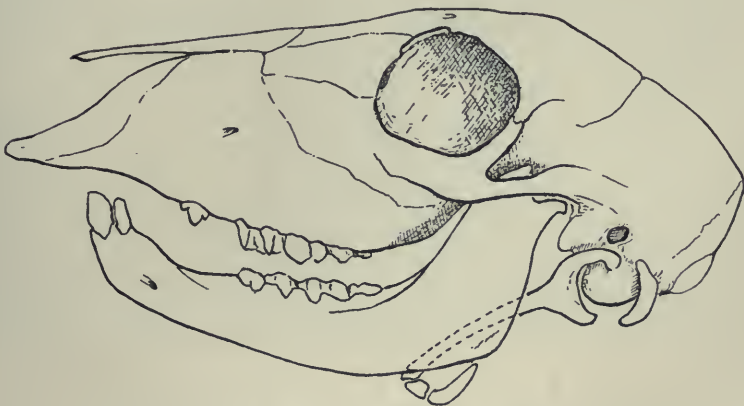


Fig. 2. Skull of "hog-jawed" sheep.

erupted. The inferior alveolar nerve appeared to be normally developed, except for the shortening corresponding to the defective development of the jaw. On opening the skull the cerebral hemispheres were seen to be fused in the median line, for the anterior three-fourths of their extent. On making a median section it appeared, however, that there was a septum of pia mater, similar to that between the posterior columns of the spinal cord occupying



the position of the great longitudinal fissure. In other respects the brain, including the olfactory lobes (fig. 3) and pituitary body, appeared to be normal. Sections of the pituitary gland were cut and stained with haematoxylin and eosin; these showed the typical structure of the gland at birth. The tympanic ossicles and tensor tympani were also normal.

One of the most instructive examples of brachygnathia which we have met with in the literature of this subject is a specimen occurring in a lamb described by Nicolas and Prenant in 1888 (fig. 4). In this case the lower jaw bone was completely absent though the tympanic ossicles, including the malleus,



Fig. 3. Skiagram of head of "hog-jawed" sheep.

with its muscle, the tensor tympani and the pterygo-palatine region were present. Anteriorly the floor of the mouth was absent so that the vault of the palate was freely exposed to the exterior. A buccal cul-de-sac passed backwards from the open part of the mouth cavity as far as the palatopterygoid region (fig. 5) where there was a blind recess immediately behind the palate bones; posteriorly to this was a small nodular projection and behind this a communication between the mouth and nasal cavities. The nasal cavities

did not communicate with the pharynx posteriorly, and the latter ended blindly below the base of the skull. In the anterior wall of the pharynx was seen the basal part of the tongue, the anterior mandibular portion of which,

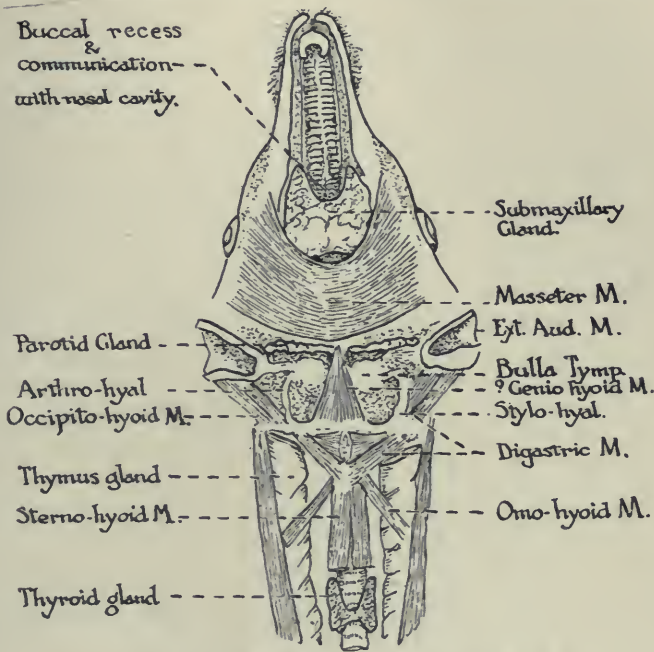


Fig. 4. Head of agnathic lamb (Nicolas and Prenant).

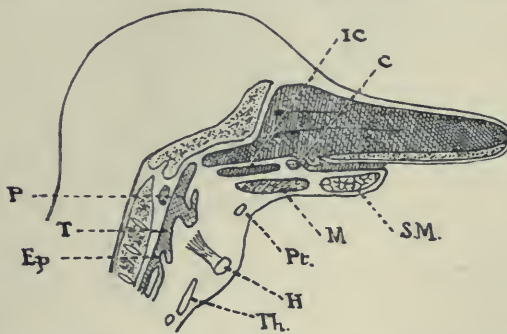


Fig. 5. Longitudinal section through head of agnathic lamb (Nicolas and Prenant).

*S.M.*, Submaxillary Gland; *M.*, Masseter; *Pt.*, Parotid Gland; *H.*, Hyoid; *Th.*, Thyroid Cartilage; *Ep.*, Epiglottis; *T.*, Tongue; *P.*, Soft Palate; *C.*, Communication between mouth cavity and nasal cavity.

together with the genio-glossi muscles, was absent. Above the basal rudiment of the tongue was a fold of mucous membrane which was regarded as the pharyngeal portion of the soft palate which contained palatine muscles belonging to the fore-gut. This the authors inferred is developed independently

of the anterior fibrous portion of the soft palate, which is formed in connection with the palato-pterygoid elements. Between these two parts of the soft palate was an interval which presented anteriorly the communication between the buccal and nasal cavities mentioned above. Behind this was a fibrous mass enclosing an intermediate cavity, the roof of which was formed by the floor of the nasal fossae while its floor was continuous with the shortened floor of the buccal cavity and with the lower lip. This intermediate cavity was regarded by the authors as a part of the pouch of Rathke cut off from the pharyngeal end of the stomodaeum. A dissection of the floor of the mouth and front of the neck revealed a glandular mass formed by the fused sub-maxillary salivary glands; behind this a muscular mass consisting of the two masseter muscles fused across the middle line, and on their deep aspect, the imperfectly developed pterygoid muscles. Posteriorly to the muscular band was a gland on each side; this, judging from its position between the masseter and external auditory meatus, was believed to represent the parotid salivary gland. The external auditory meatuses were situated below the usual level and were nearer the median plane than is normally the case. The tympanic bullae situated close to one another were separated by a triangular muscular mass, attached posteriorly to the hyoid bone and representing the mylohyoid and geniohyoid muscles. This case and others which we shall describe later opens up the extremely interesting and much debated question of the relation of the tympanic ossicles to the development of the lower jaw, and also of the developmental relations of the soft palate and the pouch of Rathke, the consideration of which will be found in the summary at the end of the paper.

A further degree of the deformity is seen in the head of a lamb of which there are two specimens in the Museum of the Royal College of Surgeons, England. The first of these, No. 186, shows the soft parts which have been removed from the skull. The defect is unilateral and is an example of the type of deformity called Hemignathia. The principal points noted in the catalogue are the following: The right half of the inferior maxilla, and the right palate and malar bones are absent. The cavity of the mouth is completely open on this side and is continuous with the first visceral cleft, the posterior boundary of which is formed by a smooth groove of mucous membrane, sloping outwards, backwards and upwards to the pinna, probably representing the lining membrane of the Eustachian tube and external auditory meatus. The tongue is well developed but divided into three lobules. A wide median cleft extends through the posterior half of the palate. The lower eyelid on the right side is undeveloped and the eye is only separated by a thin band of mucous membrane from the floor of the mouth.

In the second specimen, No. 187 (fig. 6), which is the macerated skull of the same lamb, it will be noticed that all the bones developed in the right half of the first visceral arch are completely absent. The malar bone and the pterygoid process are also wanting. The right premaxilla is well formed and continued somewhat further backwards than on the opposite side. The different



portions of the temporal bone are all represented but are not well developed, the tympanic bone is especially small and the bulla rudimentary. The external auditory meatus is represented by a small foramen. There was no trace of a tympanic membrane nor of the bones of the internal ear. A noticeable feature of this specimen is that the right orbit is directed downwards and medially towards the central axis of the skull. This displacement towards the

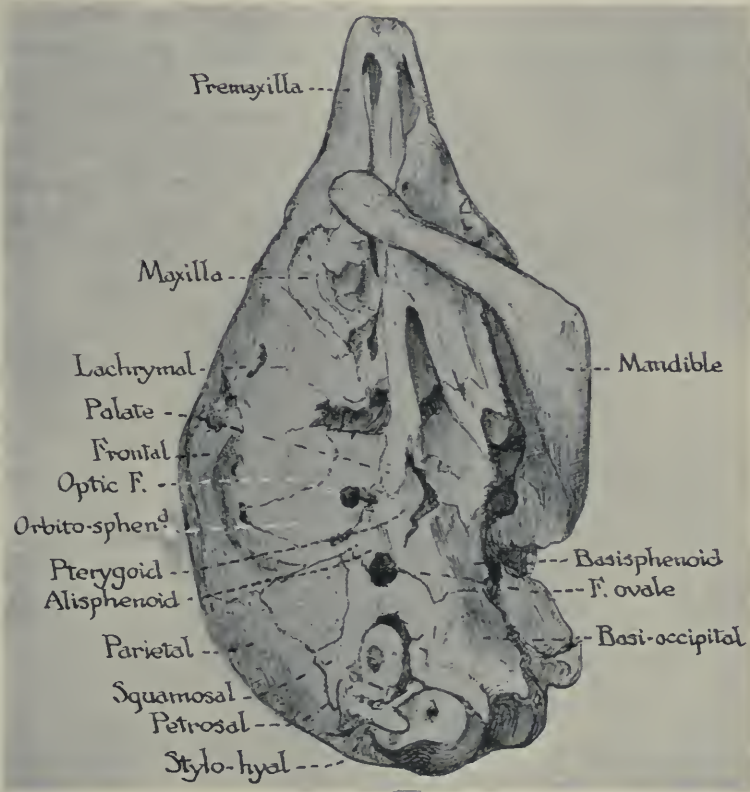


Fig. 6. Unilateral agnathia in a lamb.

median plane indicates a stage in the development of cyclopia. Owing to the unilateral nature of the defect, the opposite side being normal, this specimen is of exceptional value, for by comparing the two sides, the relationship of the eye and orbital cavity to the anterior nares and the mouth is very clearly indicated, and also the displacement backward of the opening of the mouth, which is caused by shortening or absence of the mandibular arch and upper jaw (see also fig. 7). It will be obvious that should the defect have been bilateral as in fig. 9, the ethmo-vomerine region would lie in front of, or would be displaced upwards above the cyclops eye to a region where a proboscis is frequently formed, the cavity of which would be completely cut off from the

naso-pharynx, by the growth of the conjoined eyeballs and optic nerve in a ventral direction, either between the fronto-nasal process and the maxillary processes, or between the maxillary and mandibular processes, as in certain cases of brachygnathia. If the mandibular processes fail completely, the cyclops eye will occupy a corresponding position behind the fused maxillary processes.

The next specimen which we shall describe (fig. 7) is the skull and skin of the snout of an agnathic lamb, presented to the Royal College of Surgeons, England, by Sir J. Bland Sutton. Teratological series 253A and 253B. It is valuable as it exhibits an intermediate stage between the type described by Nicolas and Prenant, and the following extreme forms in which

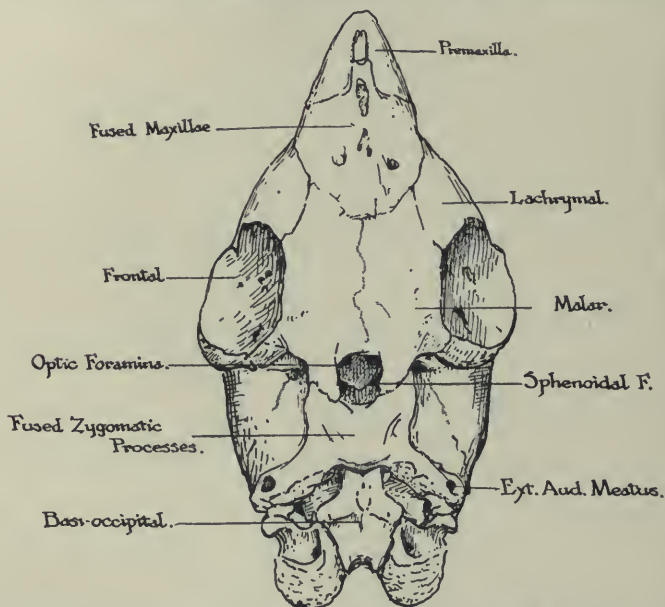


Fig. 7. Ventral aspect of the skull of an agnathic lamb, showing fusion of maxillary and zygomatic bones.

there is complete absence of the lower jaw, including the soft parts, combined with synotia or fusion of the tympanic cavities and their membranes. It also represents an intermediate stage in the development of an unusual type of cyclops, in which the cyclops eye lies behind (or below) the fused maxillae. The specimen shows an approximation of the eyes and orbits behind the maxillae, the facial surfaces of which bones are fused in the median plane on the lower or ventral aspect of the skull. The two orbits are separated from one another by the zygomatic or malar bones, which it will be observed are fused, right with left, in the median line, and by their outer borders form part of the inner margin of the corresponding orbital cavity. Each malar bone articulates in front with a lachrymal bone, and behind with the corresponding posterior or external angular process of the frontal, and also with the fused

zygomatic processes of the temporal bones (see fig. 7). Between these and the malar bones is a space in which are seen the optic foramina and the inner ends of the sphenoidal fissures. The space thus corresponds to the apices of the two orbital cavities, and the zygomatic fossae, and it will be noticed that it is continuous with a temporal fossa on each side. Anteriorly are the two premaxillae and the openings of the nasal cavities. In this specimen therefore, not only is the lower jaw completely absent, but the palate and alveolar processes are also undeveloped, a condition which will be readily appreciated by reference to the unilateral specimen (fig. 6).

A further stage in the production of the defect is illustrated by a specimen occurring in a human subject, described by Lewis Graham in *Studies of*



Fig. 8. Head of agnathic human foetus illustrating the continuation of cyclops, with defective development of the lower jaw and synotia.

*Anatomy*, University of Birmingham, 1916. In this specimen there was an approximation of the eyes towards the median plane. The nose was fairly normal in appearance and the nasal cavities communicated with the pharynx. The opening of the mouth was represented by a minute aperture, and the buccal cavity was continuous behind with the naso-pharynx. The external ears and the auditory meatuses were close together near the middle line and below the level of the mouth. The mandibular region was rudimentary and the chin absent. Dissection revealed the presence of a small bar of bone which represented the lower jaw and which was found behind a mass of fat believed to represent the sucking cushion and a muscular mass representing the masseters. The tympanic ossicles were all present but were deformed; the incus being elongated, larger than the adult bone, and exceeding in length the rudimentary mandible. The hyoid bone and its associated muscles were



present. Specimen 261, Museum, Royal College of Surgeons, England (fig. 8), represents a somewhat similar though more pronounced case of agnathia in a human subject. The eyes were fused into a single bulb presenting two corneae separated by a vertical fold of conjunctiva. The nose was represented by a small nodule having a single depression on its summit representing the fused nostrils. Below this a pinhole aperture represented the mouth. The tympanic cavities and ossicles were conjoined and there was no vestige either of the mandible, or facial axis. The eyes and ears were situated in front of the axis of the skull which is stated in the catalogue to be perpendicular instead of horizontal. The pharynx opened externally by spiracles which communicated with the exterior through the external auditory meatuses.

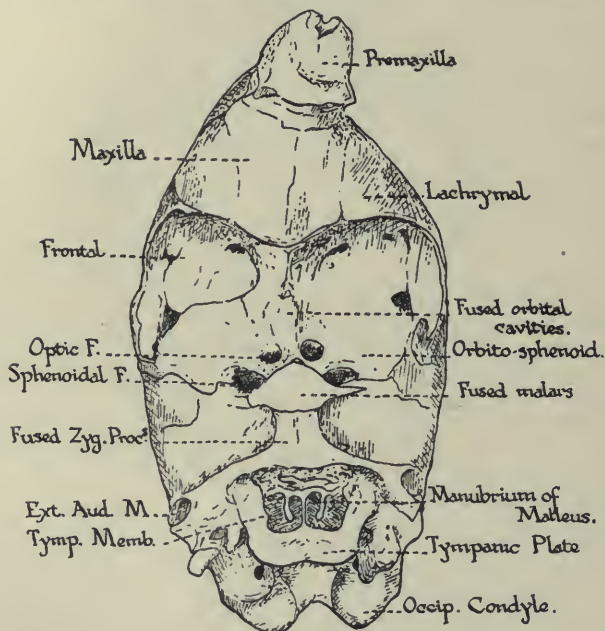


Fig. 9. Skull of agnathic lamb viewed from the ventral aspect showing fusion of the orbital cavities, and of the tympanic membranes.

Fig. 9, Teratological Series 253D, Museum, Royal College of Surgeons, England, represents a still later stage in the disappearance of the mandibular arch, namely that preceding the rare examples of total absence of the mandibular arch including the tympanic ossicles and pterygo-maxillary region, a condition which is usually associated with a complete failure in the development of the face. If this figure which represents the basal surface of a lamb's skull be compared with fig. 7, it will be at once noticed that the two orbital cavities which in fig. 7 are separated by the fused zygomatic bones are in fig. 9 joined into a single cavity bounded in front by the fused maxillae and more laterally by the right and left lachrymal bones. Behind is a triangular plate of bone formed by the fused zygomatic bones and articulating posteriorly

with the united zygomatic processes of the temporal bones, which may be traced outward and backward on each side to the external auditory meatus. The lateral angles of the zygomatic plate fail to meet the posterior zygomatic processes of the frontal bones, so that the orbital margin is interrupted in this situation. The lateral boundaries of the composite orbital cavity are constituted by the supra-orbital margins of the frontal bone. The optic foramina and sphenoidal fissures occupy approximately the same position as in the stage represented by fig. 7 but there is a marked difference in the tympanic region, where the two tympanic membranes have coalesced edge to edge in the median plane and are framed by a U-shaped bar of bone formed by the fusion of the two tympanic plates. In the centre of each half of the common tympanic membrane is the manubrium of an imperfectly developed malleus, above which appears to be a rudimentary incus.

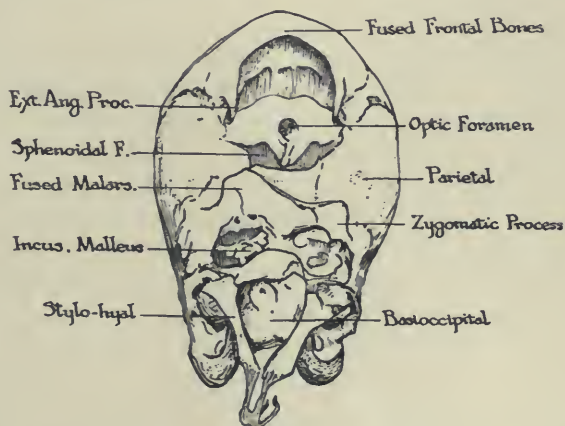


Fig. 10 Skull of foetal lamb showing the combination of "cyclops," "agnathia," and "synotia."

In fig. 10 (Museum, Royal College of Surgeons, England, Teratological Series 268) a still higher degree of defect is represented. The ethmoidal and maxillary regions of the face are completely absent. There is a single optic foramen in a plate of bone formed by the fused orbito-sphenoids. The composite orbital cavity is bounded in front by the supra-orbital margins of the frontal bone, which have coalesced in the median line so as to form a single arch which is uninterrupted by the nasal notch and the associated nasal bones which in the sheep normally occupy this notch. The maxillary and lachrymal bones, usually found in this region, are also completely wanting. The inter-frontal suture is absent and we consider it probable that the frontal region of the brain would have been imperfectly developed and the hemispheres fused with one another. The zygomatic processes of the temporal bones project forwards and inwards behind the common orbital cavity, where they articulate with a projecting plate of bone, formed by fusion of the two zygomatic bones. Behind this is an irregular mass of bone formed by the imperfectly developed

tympanic ossicles. This is bounded posteriorly by a curved bar of bone representing the tympanic plates.

#### SUMMARY.

It is evident that the specimens we have described illustrate the mechanical effects resulting from the absence or imperfect development of the central region of the cranio-facial axis. If the central parts are absent, the lateral parts grow forwards in contact with each other and fuse in the median plane. Thus if the fronto-nasal process fails to unite with the maxillary processes, the former with the contained ethmo-vomerine cartilage and lateral nasal cartilages may be displaced upwards in the form of a proboscis. If the frontonasal process is imperfectly developed, or absent, the two orbital cavities will be joined into a single chamber containing the two eyeballs, lying side by side, or fused medially into a single organ giving rise to the condition of cyclopia.

In this defect the anterior parts of the maxillary processes are often fused in the median plane, the philtrum of the upper lip and the premaxilla being absent. Should the mandibular processes be defective and the buccal part of the tongue which is normally developed in association with the central part of the mandibular arch and projects upwards between the palatal processes be absent, there will be nothing to prevent the palatal processes from uniting with one another before they are fully developed; or should they fail to be developed the maxillary processes will unite in such a way that the bodies of the maxillae will be fused in the median plane and the respiratory part of the nasal cavities will be entirely absent. Moreover it will be seen on referring to fig. 7 that in some cases the alveolar borders of the maxillae will be rolled inwards and join beneath the palatal region.

There is also in many of these cases an alteration in the direction of the prechordal or trabecular portion of the cranio-facial axis. This is usually represented by a line drawn from the prosphenoid (tip of the sphenoidal spine) to the nasion. The angle which is formed by the meeting of this line with a line passing from the prosphenoid to the basion, indicates the direction of the prechordal section of the axis. In the adult human subject this angle is about  $140^\circ$ , in the foetus at birth about  $160^\circ$  and in an embryo of 20 mm. it is about  $170^\circ$ . The acuteness of the angle contained between these two lines is evidently largely dependent on the growth of the forebrain pressing down the orbital and ethmoidal regions of the skull. Should the growth of the brain be defective, as is frequently the case in these monsters, the prechordal part of the axis will retain the embryonic position and the angle will be wide, or may disappear altogether. There is also in some cases an alteration in the angle which the basi-cranial axis forms with the longitudinal axis of the upper part of the vertebral column which may be indicated by a line passing from the tip of the odontoid process through the centre of the body of the axis vertebra. This in the adult human subject is approximately  $115^\circ$ , in the foetus at birth  $142^\circ$ ,



while in the embryo it varies markedly according to age. It is very wide in early embryos of 3-4 mm. length, it lessens as the cervical flexure develops, and then widens out again in the foetal period. The angle in these agnathic monsters is usually considerably larger than the normal angle present at birth. The presence of the tympanic ossicles in many cases of complete absence of the lower jaw suggests that these bones are developed independently of Meckel's cartilage. This supposition is in accordance with the statement made by Fuchs, that there is in the rabbit a common anlage for the malleus and incus, and that this arises independently, chondrifies from a separate centre, and becomes secondarily fused with Meckel's cartilage. The latter, according to Fuchs, arises from a centre which lies in the region where the temporo-mandibular joint is afterwards differentiated, and from which the articular part of the squamosum also arises.

The tympanic ossicles, however, when present in cases of agnathia are often imperfectly developed and are sometimes absent.

Without entering into a consideration of the difficult problem of the morphology of the tympanic ossicles and the question as to whether or no the joint between the incus and malleus represents the reptilian mandibular joint, it may be worth while pointing out that the presence of these ossicles in many cases of agnathia in which there is a complete absence of the mandible and the soft parts associated with it, appears to support the statements of H. Fuchs, with respect to the origin of the malleus and incus from an independent prechondral rudiment which chondrifies separately, and subsequently fuses with the proximal end of Meckel's cartilage.

#### INHERITANCE.

The inheritance of congenital deformities is classed by J. Arthur Thomson, under the following headings:

- (1) Inheritance of defects, such as albinism, loss of horns in cattle, or absence of the ears, or tail.
- (2) Imperfections due to an arrest of development.
- (3) Multiplicities.
- (4) Malformations of parts.

Of these, the second class, namely, imperfections due to an arrest of development is the type of deformity which we have been studying.

Thomson's conclusions agree with those which we have arrived at independently and from a different standpoint. He believes that the persistence in the child at birth of a condition such as hare-lip, cleft-palate, or spina bifida which represents a transient stage in the development of the embryo may be the result of inadequacy of nutrition or deficient developmental vigour. These factors are responsible for the non-union of parts which normally unite with one another, and also the failure in development of certain parts, and he points out that although these abnormalities may occasionally recur repeatedly in a family tree it seems probable that what is really inherited

is a deficiency in developmental vigour accentuated by nutritive defects on the part of the mother, during the period of gestation.

These conclusions are supported by the views expressed by Sir Arthur Keith in his popular lecture on Evolutionary Wounds, delivered at the meeting of the British Medical Association in July, 1921, at Newcastle, namely that the union of parts in the embryo is with the exception of the vascular changes very similar to the union which takes place in the healing of a wound in post-natal life. As the healing of a wound in post-natal life may be interfered with by a local or constitutional cause, so mechanical or constitutional causes may prevent the union of parts in the embryo.

With reference to cleft-palate or hare-lip, the authors in Holmes and Hulke's *System of Surgery* remark, "We cannot state that congenital cleft of the mouth or lip is a common occurrence as a result of hereditary transmission. It is rare to observe one of the parents and the offspring affected, although brothers and sisters of the same family constantly present different conditions of the deformity. How far civilization or crowded populations may influence congenital deficiencies in the human subject is a question to be hereafter worked out, but it is a curious fact that most of the lions caged in the Zoological Gardens of London, are born with defective palates, and consequently die soon after birth.—It appears that it is not usual for a lion family in a state of confinement to have their young similarly affected, but this congenital defect is restricted to the lions kept in the Regent's Park as if some local influence were instrumental to this end."

In view of the results which have been obtained by the American experimental embryologists, who have shown that defects in the development of the face and other parts may be produced by malnutrition, we considered it important to come to a definite conclusion as to whether these defects are truly inherited or not and also if certain cases are truly inherited, what is the percentage number of cases which should be classed as due to germinal inheritance, and what the number due to inheritance of disease, or degeneracy of the stock.

By consulting the standard surgical textbooks we found expressions such as the following in favour of the hereditary transmission of the defects of hare-lip and cleft-palate, namely: "a well marked hereditary tendency," "frequently transmitted from one generation to another," "little that is definite can be stated, except that heredity is an important factor."

We have examined the records of 554 cases of hare-lip and cleft-palate, which have come under treatment at the following hospitals, King's College, St Thomas's, Hospital for Sick Children, Great Ormond Street, and Middlesex, and as a result of the inquiry we have found that there are only two cases (0.35 per cent.) in which it has been recorded that a parent having hare-lip or cleft-palate has had a child with a similar defect. There were instances of several members of a family being the subjects of a congenital defect and there

were a few cases in which a cousin, uncle, aunt, grandparent, or other more remote relative was affected. The congenital defects of development were not always of the same kind, e.g. in a single family a child with hare-lip might have a brother or sister with club-foot or spina bifida.

In each of the two cases recorded in which a parent showed the deformity it was the mother who was affected, and the defect was on the same side as in the child. In one case which was successfully treated by Mr Barrington Ward, at the Hospital for Sick Children, Great Ormond Street, no other member of the family or any relatives were known to be affected. In the other case, operated on by Mr Tyrell Gray in the same hospital (see pedigree fig. 11), the great-great-grandfather and a cousin of the grandfather's were said to have had the same deformity, and the hare-lip which in the child, a girl, was on the left side, was present on the same side in the mother and an uncle.

A few cases have been recorded by Clement Lucas and others in which there is an association of absence of the lateral incisors, and other irregularities of dentition with cleft-palate and hare-lip, and we have ourselves come across one case not included in the above series in which a grandparent had a cleft-palate, and two grandchildren had hare-lip and cleft-palate, two grandchildren had absence of the upper lateral incisors, and three others malformed

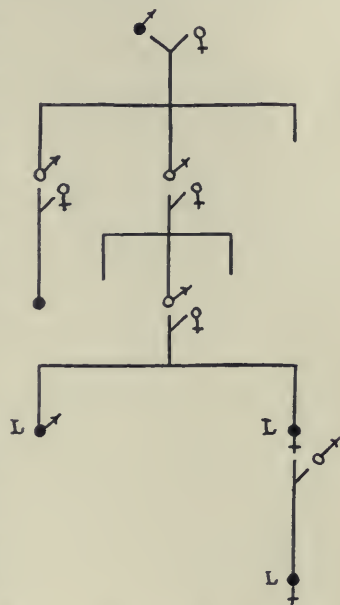


Fig. 11. Pedigree of a girl operated on for hare-lip by Mr Tyrell Gray. *L* indicates that the defect was on the left side.

teeth. Another case which is of interest in connection with the association of defects in the development of the brain, with defects in the development of the face, is one in which it was stated that the father and grandfather of a child with cleft-palate suffered from a slight impediment in speech.

In those cases in which no history of the deformity has been present in the family, the following conditions or circumstances affecting the mother have been present or have been alleged as causes of the deformity:

Fright, e.g. air raids.

Mental impressions, e.g. the father of a child with hare-lip had a scar on his lip, caused by an accident when a boy. It was on the same side as the hare-lip in the child. During gestation the mother had noticed and been impressed by changes in the colour of the scar, due to congestion.

Injury to the mother during gestation, e.g. kicks in the abdomen, and falls.

Disease and ill-health, e.g. ulcerated throat, tonsilitis, history of previous



abortions, indigestion, gastro-enteritis, chronic constipation, heart disease, mental worry.

One of the best and most complete investigations into the frequency of an hereditary history in cases of hare-lip and cleft-palate, is that of Rischbieth's in the *Treasury of Human Inheritance*, part iv, 1910, of the Memoirs published by the Eugenics Laboratory, University College, London. In this article the percentage number of cases of hare-lip and cleft-palate to the General Population is fully discussed and estimated at 0.057 per cent. and also the frequency in special classes, e.g. prostitutes, in which it appears to be very common, 9.3 per cent. The relative frequency of the defect in different relatives has also been determined, and from these tables it is seen that about two-thirds of the cases classed as hereditary, are instances of brothers or sisters being affected. In many of these cases there is no history of the parents or any other relatives being affected, and we believe that they may be explained otherwise than by germinal inheritance, namely by assuming that the nutrition of the embryos in utero is defective, owing to impaired health, degeneracy, or disease present in the mother. There thus remains only a small percentage of the total number of cases in which the defect can be said to be transmitted from parents to children and it is probable that a considerable number of these may be attributed to inheritance of disease, or degeneracy of the stock. Thus if there is no history of the defect being present in the family, and *the parents are healthy*, if one of the parents is affected with hare-lip or cleft-palate, the likelihood of a child being similarly affected is very small, and since the results of operations on hare-lip are so good, it is doubtful whether, apart from all ethical considerations, restriction of childbirth, with the object of preventing reappearance of the defect in the family should be countenanced by the medical profession. Although instances do occur, the odds against its reappearance provided the health of the parents is sound, is probably more than a hundred to one.

Some light on the effect which artificial conditions may have on the teeth and jaws, may be obtained by a study of domestic animals, e.g. the Pekingese dog.

The evolution of the Pekingese type of dog is obscure. Collier states that about 500 years B.C. it is recorded that dogs were used for sporting purposes. "Some of these were probably small dogs for it is mentioned that after the day's sport one kind of dog followed his master's chariot, while those having short mouths were carried in carts." Collier, however, believes that the special Pekingese varieties have been derived at a much later period from dogs of the spaniel type, imported into China from Europe. The breeding and care of these dogs has been entrusted to eunuchs in the Imperial Palaces, and the methods employed have been kept strictly secret. It is known, however, that one of their main objects was to produce a lion-dog which would resemble the Chinese lion which symbolises the spirit-lion of the Buddhist and Lamaist religions. The peculiarities of this Chinese-lion are familiar to

all students of Chinese art, and it is evident that the dog breeders have attained very considerable success in reproducing the distinctive features of their model. It is probable that the chief methods of securing their object has been selection, and in-breeding. Other ways of modifying the development of the body were employed, namely: to allow the dog to take little exercise from the third month to maturity, with the idea of lessening the appetite, and thus retarding growth: to hold the growing specimen in the hand for days at a time, inducing, by gentle pressure of the fingers, a slight exaggeration of width between the shoulders. One method alleged to have been employed for arresting development was, as in the case of foot-binding, particularly cruel. It is said that the puppies when small were enveloped in wire cages closely fitting the body and not removed until maturity was reached. "Other breeders fed their puppies from a flat plate, or encouraged them from the age of three months upwards to bite pig-skin stretched on a board." "Others will massage the nose daily with the object of restraining growth of this 'obstinate organ' which only too often appears to be but little stunted after this persistent snubbing."

It is probable that the stunting in growth produced by the more barbarous of these means would act on individual specimens only, but in whatever way the stunting of the development of the body as a whole, or of the nose in particular, has been brought about, it is obvious that it is inherited, and that if these pampered dogs were left to fend for themselves, they would be unable to survive in a wild state. They, like hot-house plants, have been modified by external conditions, their food has been found for them, they have lived a life of indolent luxury, and the modifications induced, have been inherited. Although doubtless selection has been employed it is probable that the variations which are selected have arisen as modifications produced by artificial means.

#### CONCLUSIONS.

In view of the conditions described above we have come to the following conclusions:

(1) The experimental work of McClendon, Stockard and others on the larvae of anamniota indicates that injury or poisons acting on the growing larva will produce effects which vary according to the period of growth and the intensity of the injury inflicted, or poison administered; and we believe that similar deleterious influences will interfere with the normal growth of the embryo in mammalia; and that ante-natal deformities such as cleft-palate, hare-lip, agnathia and cyclops are usually the result of imperfect nutrition, or malnutrition of the embryo.

Congenital defects in animals appear chiefly in those which are reared in an artificial environment; such as lions bred in confinement, and domesticated animals.

(2) That the nature and degree of the deformity depends upon the part

primarily affected, and the secondary mechanical results which follow are due to the imperfect development of one part, e.g. fusion of the maxillae, following failure in development of the ethmo-vomerine region of the face.

(3) Direct inheritance of ante-natal deformities appears to be the exception rather than the rule. In 554 cases of hare-lip and cleft-palate we found only two in which it was recorded that the deformity was present in one of the parents.

(4) Ante-natal defects of development appear to be the result of the same conditions which in some subjects may produce defect in growth, after as well as before birth, for instance, deformities of bone in rickets or craniotabes in syphilis.

(5) We believe that the defects in growth of the face and lower jaw are usually associated etiologically with defective development of the brain; for instance cyclops with defective growth of the fore-brain; otocephaly and agnathia with maldevelopment of the hind-brain.

In conclusion the authors of this paper wish to express their thanks to the Staff and Members of the Committee of King's College Hospital, the Hospital for Sick Children, Great Ormond Street, The Middlesex Hospital, and St Thomas's Hospital, for their kind permission to use the records of their cases, and also to Mr George Waugh and Mr Courtenay Mason for their interest and help in the investigation.

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# NOTES ON THE FORMATION OF THE CARDIAC SEPTA IN THE CHICK

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G. LINDES<sup>(1)</sup> investigated many years ago the development of the heart, and described the formation of the cardiac septa noticing the analogy which exists between the development of the heart of birds and that of mammals. Afterwards, J. Masius<sup>(2)</sup> confirmed many points of the dissertation by Lindes and described in detail the development of the cardiac septa in the chick and their completion. Later still, F. Hochstetter<sup>(3)</sup> wrote on the same subject minutely and made clear the development of the septum in the truncus and bulbus, in particular. Recently, F. R. Lillie<sup>(4)</sup> has given an account of the formation and completion of the cardiac septa, in his book; but some points still remain obscure or insufficiently illustrated. On the suggestion of Prof. E. S. Goodrich I have also studied this subject in the Department of Zoology and Comparative Anatomy, Oxford.

I am greatly indebted to Prof. E. S. Goodrich for continuous help and advice during the progress of this study; and for permission to use his preparations, I take this opportunity of expressing my sense of gratitude.

The object of this study was to make clear the formation of the cardiac septa of the heart; in particular their completion. So far as I observed, the formation of the cardiac septa occurs as already described by Masius<sup>(2)</sup>, Hochstetter<sup>(3)</sup> and Lillie<sup>(4)</sup>; especially, concerning the development of the aortico-pulmonary septum, my observations agree with the description given by the latter two authors. But in respect to the completion of the cardiac septa, their view is a little different from my observation.

According to Masius, the completion of the cardiac septa is carried out by the fusion of the two endothelial ridges in the bulbus, which are arranged in the direction of the free border of the interventricular septum, and also their fusion with the border of the interventricular septum. Hochstetter and Lillie described a groove in the endothelial cushion, which has an important relation in enabling the aorta to continue to the left ventricle (see below).

They stated that the right side opening, towards the right ventricle, of the groove of the endothelial cushion is bridged over by an extension of the right ventral portion of the endothelial cushion, as far as the right side of the septum in the bulbus, and that thus the completion of the cardiac septa is effected. Lillie has not given an account of the formation of the groove in the right side of the cushion, but Hochstetter has described it. According to him, by fusion of the dorsal portion of the interventricular septum with the right

edge of the endothelial cushion, the wide interventricular foramen becomes considerably narrowed. Consequently the blood from the left ventricle, forced out by each systole, digs out a groove in the ventral portion of the exceedingly plastic endothelial cushion, which appears over the interventricular foramen.

The completion of the cardiac septa is perfected on the 7th day of incubation, and is effected by the union of the interauricular septum, the interventricular septum and the aortico-pulmonary septum, by the mediation of a large septum derived from the endothelial cushion. All these septa are formed almost synchronously, but the development of the interauricular septum is slightly in advance of the development of the others, and the cushion septum appears in the atrio-ventricular canal, i.e. in the opening between the primitive atrium and ventricle.

The three primitive partitions develop in general from the periphery towards this septum. In the interauricular septum, there appear several perforations secondarily, and these foramina do not close up till later; consequently the free communication between the right and left chambers of the heart is seen, even after the completion of the cardiac septa has taken place.

During the development of the heart, there occur some changes of the positions occupied by the chambers of the heart in relation to the axes of the embryo; but for simplicity, I show in the following description, the apex of the heart as posterior, and the bulbus face of the heart as ventral, in position.

*The interauricular septum.* The beginning of the interauricular septum is seen already in the embryo of 4 days, as a thin myocardial partition, and it develops from the periphery towards the centre of the heart, i.e. towards the atrio-ventricular canal. The dorsal portion of the interauricular septum arises at a point between the aperture of the sinus venosus and the opening of the pulmonary vein. As the development of this septum progresses centrally from the periphery, it has a free border concave towards the atrio-ventricular canal, and there remains a wide communication between the right and left chambers of the heart. In the embryo of 5 days, the interauricular septum is almost completed, but several perforations are seen in it.

*The aortico-pulmonary septum.* This septum is formed in the truncus and bulbus arteriosus, dividing them into two arteries, the aorta and pulmonary artery; and as it grows more slowly than the others, in the 5 day embryo, a part of this septum is only developed. Originally, this partition develops as three parts, the anterior part in the truncus, the middle part in the distal portion of the bulbus arteriosus and the posterior part in the proximal division of the bulbus, and these three parts unite to form a continuous septum, which runs somewhat spirally from before backwards. As the formation of the anterior part of this septum occurs earlier than that of the others, it is well developed already in the embryo of 5 days and 12 hours of incubation, extending from the anterior end of the truncus to the distal portion of the bulbus and separating the aorta and the pulmonary artery. In the distal portion of the bulbus, there appear three longitudinal endocardial ridges and they all run



from before backwards, taking very slightly spiral courses. The largest one of these ridges appears dorsally and the other two lie ventrally and side by side, the right one being larger than the left. The dorsal ridge extends between the ventral two ridges and fuses with them; but as it approaches the proximal portion of the bulbus, the dorsal ridge comes to extend a little obliquely from left to right and fuses with the ventral right ridge more than with the ventral left. Thus the middle part of the aortico-pulmonary septum is formed and this septum continues anteriorly to the septum of the truncus. The posterior part of the aortico-pulmonary septum is formed by the fusion of two longitudinal endocardial ridges, which appear in the proximal division of the bulbus. These ridges take a bilateral position at the posterior end of the bulbus, and the left one of them continues anteriorly to the dorsal ridge of the distal portion of the bulbus, and the right ridge is the prolongation of the right ventral ridge of the distal portion of the bulbus. In the proximal part of the bulbus, a small accessory ridge is formed in addition to the above-stated two ridges. I clearly observed the above-stated condition in an embryo 5 days and 12 hours old.

The aortico-pulmonary septum runs spirally from the anterior end of the truncus to the posterior end of the bulbus; hence anteriorly the aorta appears on the right of the pulmonary artery, but it takes up a position dorsal to the pulmonary posteriorly. Originally, as the bulbus arteriosus continues the right half of the ventricle, so the aorta and the pulmonary artery both open into the right ventricle before the completion of the cardiac septa; but on this completion, the pulmonary artery retains its original continuity with the right ventricle, while the aorta comes to open into the left ventricle. This is explained below.

*The interventricular septum.* At an early stage of the development of the heart, the peripheral part of the ventricular cavity becomes spongy by the formation of many ramified and anastomosing processes of the myocardium; and some of them grow longer than the others, are grouped rather compactly and are fused together at their apices along a course which runs from the left anteriorly to the right posteriorly. Thus first arises the interventricular septum. This septum grows more rapidly in the posterior and dorsal region than in the ventral, and it unites with the endothelial-cushion septum on its right side.

*The endothelial-cushion septum.* At the beginning, this septum appears as two endothelial thickenings, one on the dorsal side and another on the ventral side, in the atrio-ventricular canal. The dorsal thickening appears a little posterior to the ventral, and grows more rapidly than the ventral thickening. The ventral border of the dorsal thickening in its anterior part soon widens out laterally; consequently it becomes triangular in its frontal view. The dorsal and ventral endothelial thickenings grow larger and fuse together, and thus the endothelial-cushion septum is formed. When the fusion occurs, it takes place in such a way that the ventral thickening unites with the dorsal at its left side; and thus a very short groove on the right side of the

ventral part of the endothelial cushion is formed. This groove is closed towards the left side and open towards the right. It plays an important part in enabling the aorta to continue to the left ventricle at a later stage, when the completion of the cardiac septa occurs. As the endothelial-cushion septum develops so as to restrict the lumen of the atrio-ventricular canal, with the completion of the former, the atrio-ventricular canal is divided into the right and left narrow auricular canals respectively, on each side of the cushion. This stage is observed clearly in the embryo of 5 days.

The formation of the above described four septa is well advanced in the embryo of 5 days and 16 hours of incubation. Already, the interauricular septum is completely formed and fused up with the endothelial-cushion septum. The aortico-pulmonary septum is also completed in the truncus arteriosus

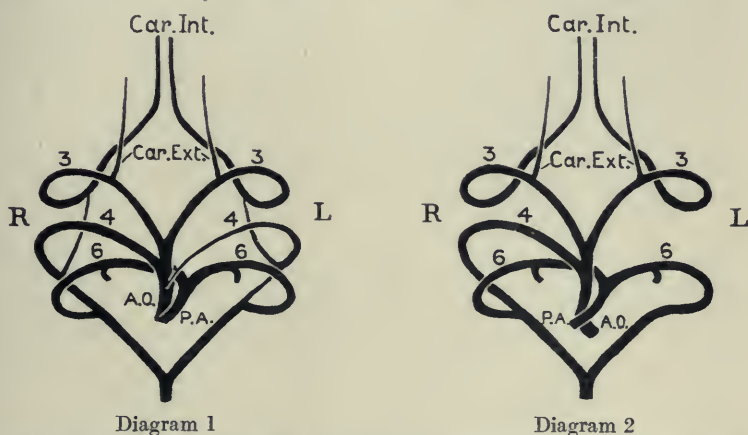


Diagram 1. The aortic arches in the embryo of 5 days and 16 hours incubation.

Diagram 2. The aortic arches in the embryo of 7 days incubation.

A.O., Aorta; Car.Ext., External carotid; Car.Int., Internal carotid; L., Left; P.A. Pulmonary artery; R., Right; 3, 4 and 6, Third, fourth and sixth aortic arches.

and almost completed in the distal portion of the bulbus, but in the proximal part of the bulbus, the fusion of the endocardial ridges has not yet occurred. As the septum develops somewhat spirally in its course, as I have stated above, the aorta and the pulmonary artery lie side by side in front (fig. 1), and the position of the pulmonary artery changes gradually towards the ventral side, as it approaches the posterior portion of the bulbus (figs. 1 and 2, Diag. 1), while at the posterior end of the bulbus the aorta appears quite dorsal to the pulmonary artery (fig. 2). The aortic division of the bulbus now opens just opposite to the groove of the endothelial cushion and just ventral to the right auricular canal (figs. 2 and 3) being separated by the right and left endocardial ridges, from the pulmonary division. The left ridge is extended backwards and is continuous with the ventral lip of the groove of the endothelial-cushion septum which is well formed at this stage; the right ridge is connected posteriorly with the dorsal lip of the groove, by the prolongation

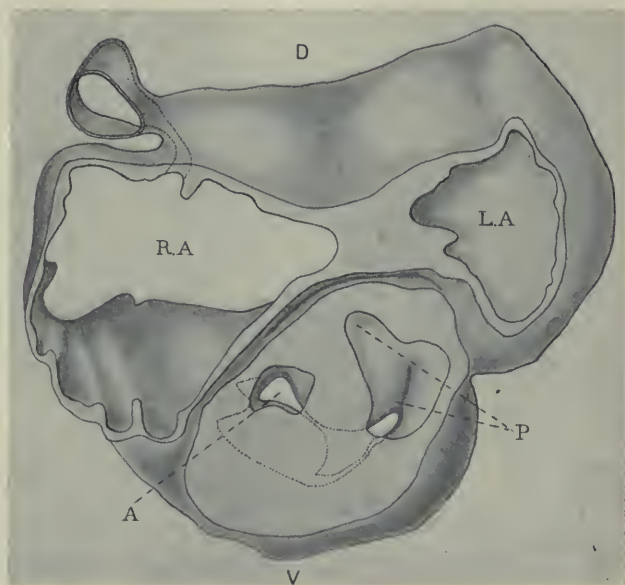


Fig. 1. Reconstruction of the anterior portion of the heart.

Figs. 1 to 3 are reconstructions of three successive portions (anterior, middle and posterior) of the heart in a chick embryo of 5 days and 16 hours incubation. They are viewed from the anterior side.

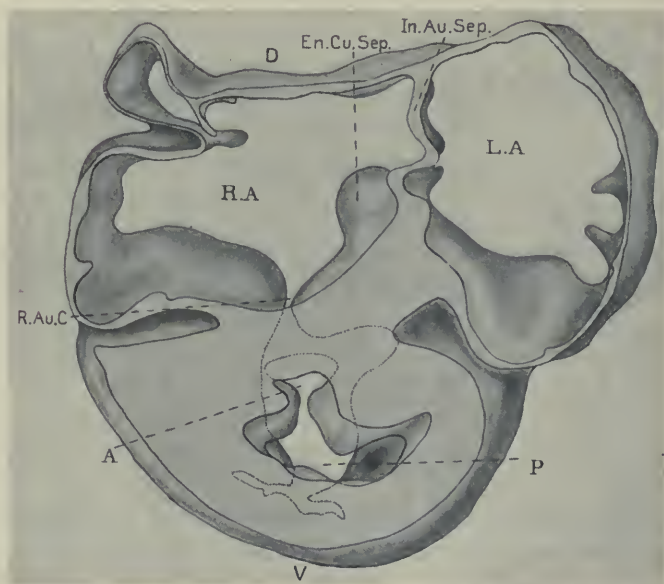


Fig. 2. Reconstruction of the middle portion of the heart, just posterior to fig. 1.



of it, at the level just anterior to the right auricular canal. At this stage, the interventricular septum is quite well developed, especially its dorsal and posterior portions are well formed (fig. 6) and already fused together with the endothelial cushion at its right side; but the anterior ventral part of the interventricular septum is still incomplete and there remains a free communication between the right and left ventricles. This interventricular foramen is bounded by the left ventral part of the endothelial cushion anteriorly, and towards the left ventricle it runs a little obliquely, from the right anteriorly to the left posteriorly; and its anterior right portion is continuous with the groove of the endothelial cushion (fig. 4).



Fig. 3. Reconstruction of the posterior portion of the heart, just posterior to fig. 2.

The endothelial-cushion septum is also well developed at this stage; its groove, which is situated just opposite to the opening of the aortic division of the bulbus, being quite well formed. A part of this groove is already changed into a short canal, which is formed by the fusing together of the dorsal and ventral lips of the groove, and is beginning to accomplish its important part in perfecting the connection between the aorta and the left ventricle; the myocardial processes, forming the interventricular septum, stretch from the ventral wall and fuse with the endothelial cushion at the ventral lip of the groove (fig. 5).

During later development the fusion of the two lips of the groove into a canal continues forwards while the formation of the aortico-pulmonary septum proceeds backwards. Finally the aortico-pulmonary septum and the

portion of the endothelial cushion formed by the closure of the groove, meet together and fuse. In the embryo of 6 days, this condition is well shown; there appears a narrow communication between the aorta and the pulmonary artery, at the hind end of the bulbus arteriosus (fig. 7). This communication shows the place where the aortico-pulmonary septum and the part of the endothelial cushion just described met and fused.

While the aorta loses its original communication with the right ventricle and attains its new connection with the left ventricle, the pulmonary artery retains its original continuity with the right ventricle; since the opening of the pulmonary artery appears ventrally to that of the aorta and to the right of the interventricular septum.

Thus the completion of the cardiac septa is effected by the fusing together of three primitive partitions, i.e. the interauricular septum, the aortico-

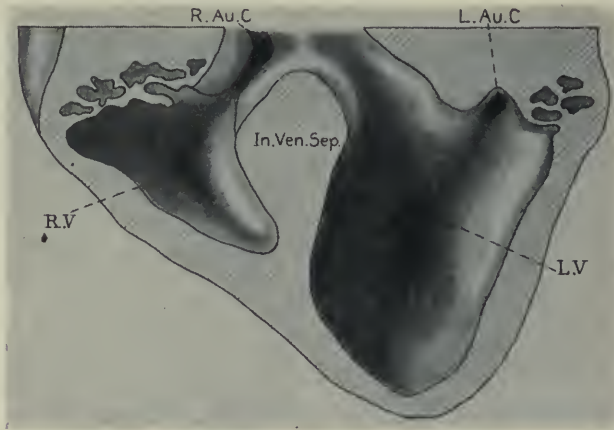


Fig. 4. Reconstruction of the dorsal part of fig. 3. The direction of the plane of section is shown by a line *xy* in fig. 3.

pulmonary septum and the interventricular septum, with the help of the endothelial-cushion septum; and it comes about that although the aorta continues into the right ventricle with the pulmonary artery primarily, it comes to open into the left ventricle secondarily. This is brought about by the fusing together of the interventricular septum with the endothelial-cushion septum at the right side of the latter, and by the prolongation of the aorta. The aorta is prolonged by being continued into the perforation of the endothelial cushion and the communication between the right and left ventricles, due to the incomplete development of the interventricular septum at its anterior and ventral part (Diag. 2).

In the embryo of 7 days of incubation, the changes above stated have come to an end; consequently the completion of the cardiac septa appears to be effected during the period between 6 and 7 days of incubation.

After the completion of the cardiac septa has occurred, the left systemic

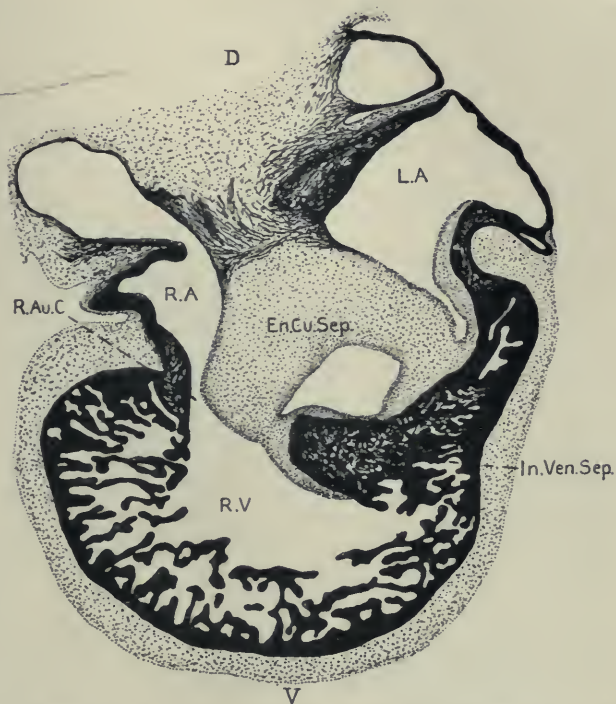


Fig. 5. Transverse section at the level where the dorsal and ventral lips of the groove of the endothelial-cushion septum fuse.



Fig. 6. Transverse section more posterior than the section shown in fig. 5.



arch has entirely disappeared and the connection between the upper ends of the third and fourth aortic arches are also quite obliterated. The right systemic arch alone remains, and the sixth arch is strongly developed on both sides (Diag. 2).

The obliteration of the left systemic arch seems to occur during the period between 5 days and 6 days of incubation. In the embryo 5 days old, the

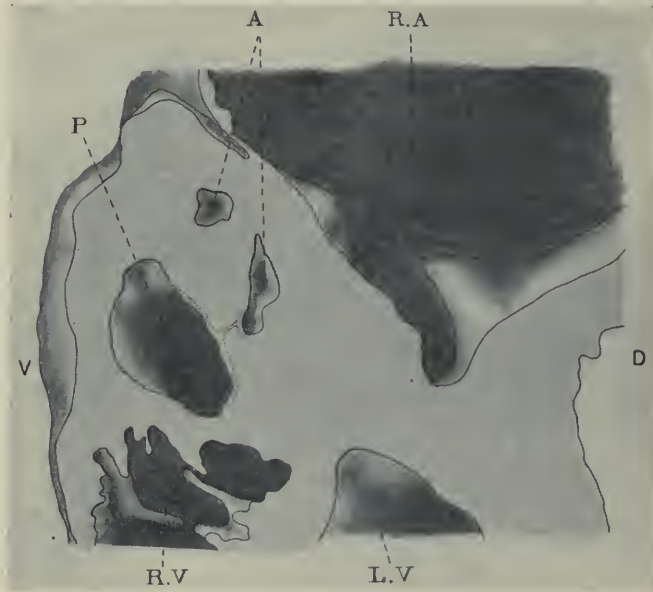


Fig. 7. Reconstruction of the posterior part of the bulbus in the embryo of 6 days incubation, showing a narrow communication between the aorta and the pulmonary artery.

systemic arch is equally well formed on both sides; but the left systemic arch becomes narrower than the right one and its connection with the bulbus becomes especially very narrow in the embryo 5 days and 16 hours old (Diag. 1). The left systemic arch entirely disappears in the embryo of 6 days of incubation and the same condition of the aortic arches as in the embryo 7 days old is seen. Since the ventral aortic trunk is never subdivided the left systemic arch disappears without the trunk passing through a Crocodilian stage.

#### SUMMARY.

1. The completion of the cardiac septa is effected by the fusion of the three primitive (interauricular, interventricular and aortico-pulmonary) septa with the help of the endothelial-cushion septum.

The former three septa develop from the periphery towards the latter in the atrio-ventricular canal, and the development of the interauricular septum is slightly in advance of that of the others.

2. On the completion of the cardiac septa, the aorta attains its secondary

continuation into the left ventricle. This occurs by the fusing together of the interventricular septum with the endothelial cushion at the right side of the latter and by the prolongation of the aorta. The aorta is prolonged by being continued into the perforation of the endothelial cushion and the interventricular communication. The former is formed by the closure of the dorsal and ventral lips of the groove in the endothelial cushion.

This groove is formed by the uniting of the ventral endothelial thickening with the dorsal thickening at its left side.

3. The left systemic arch disappears a little earlier than the completion of the cardiac septa and without the ventral aortic trunk passing through a Crocodilian stage.

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#### ABBREVIATIONS

A. aorta; D. dorsal; *En.Cu.Sep.* endothelial-cushion septum; *In.Au.Sep.* interauricular septum; *In. Ven. Sep.* interventricular septum; L.A. left auricle; L.Au.C. left auricular canal; L.V. left ventricle; P. pulmonary artery; R.A. right auricle; R.Au.C. right auricular canal; R.V. right ventricle; V. ventral.

# VARIATIONS IN THE REGION OF THE FORAMEN MAGNUM

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## VARIATIONS IN THE REGION OF THE CRANIO- VERTEBRAL BOUNDARY

MORE than a century has passed since a modification of the base of the skull was first noted. Until 1904 the various abnormalities were merely recorded and in that year Professor Kollmann introduced the controversial element by the suggestion that some of the appearances seen in the region of the foramen magnum were indicative of a "manifestation of an Occipital Vertebra," that is, a regressive in contra-distinction to a progressive change represented by an assimilation of the atlas into the skull base. The idea at the base of the contention is that the junction of skull and spinal column is not an absolutely fixed point in ontogeny any more than in phylogeny. In all amniota three spinal segments have been taken into the cranial base. These are represented in ontogeny by mere vestiges.

The vertebral column as a whole is extremely liable to variation both as regards the total number of segments and the number of segments in the various regions. Variation is seen especially at the caudal end, but it has been stated by Dwight that where there is alteration in one region of the vertebral column there is compensatory variation in other regions. I would add that at the cranio-vertebral boundary there may be compensatory variations in adjoining segments of the same region.

From time to time rules for guidance in the distinction between manifestation of a vertebra and assimilation, in the more complicated cases, have been laid down. Kollmann considers that the shape and curvature of the articular surfaces on the skull base are the essential aids, while Swjetschnikow asserts that the absence of the sulcus for the vertebral artery and the foramen in the transverse process with absence of the anterior atlanto-occipital interval are indications of manifestation of an occipital vertebra.

In this paper I propose to describe a series of specimens belonging to the Anatomical Museum of Glasgow University showing various degrees of variation in the region of the base of the skull, and then to consider how far the facts agree with the opinions which have been expressed on the subject. The series presents so complete a sequence that it seems well worth careful description and illustration.

While there are several specimens in the Museum showing fusion of the atlas to the skull and also of groups of other vertebrae, I shall consider here only



those cases which are at least not definitely due to post-natal pathological causes.

Of all variations which occur in the atlas, the most common are in the direction of reduction except perhaps in those cases in which the groove for the vertebral artery on the superior aspect of the posterior arch of the atlas is converted into a canal by the development of a spicule of bone, a condition fairly constant in most mammals and corresponding to the superior oblique process<sup>1</sup>.

The part which is most commonly absent is the posterior arch of the atlas<sup>2</sup> and therefore in those cases in which the occipital bone is modified we should expect to find the representative of a posterior arch least in evidence.

*Specimen I.* This specimen closely resembles that illustrated in fig. 1. The anterior arch of the atlas is strongly developed and from the upper border of the anterior tubercle a small rounded pillar of bone extends upwards to fuse with a similar process springing from the under aspect of the basi-occipital 2 mm. to the right of the median plane and 6 mm. anterior to the margin of the foramen magnum. A second process similar to the above rising 5 mm. to the left of the median plane on the basi-occipital passes obliquely downwards and inwards but fails to reach the upper border of the anterior tubercle of the atlas. The right process divides the anterior atlanto-occipital interval into two compartments, the left compartment being further incompletely subdivided by the left process. This represents the first stage towards obliteration of the anterior atlanto-occipital interval. The superior articular process of the atlas is fused with the occipital condyle on both sides. On the right side the joint cleavage is indicated and shows the occipital condyle to have been convex downwards. On the left side the articular interval is obliterated.

The posterior arch of the atlas is well formed, measuring 13 mm. at its deepest point. The posterior margin of the foramen magnum is very irregular and in the median plane the apex of a triangular downgrowth of bone is in contact with, but not fused to, the upper border of the posterior arch of the atlas. This irregularity indicates that ossification has been extending into the posterior atlanto-occipital membrane. The sulcus for the vertebral artery is well marked on both sides.

On the left side a well marked process of bone extends downwards from the jugular portion of the occipital, the paramastoid or paracondyloid process. This process is 15 mm. long and 13 mm. thick and on its medial side is fused with the transverse element of the transverse process of the atlas which is broadened out on its superior aspect to form a pillar of bone continuous with the paramastoid process. On the lateral side of this pillar a suture indicates the union of the two processes. On the right side of the vertebra the transverse element is more prominent than normally, but there is no indication of a paramastoid process. The costal element of the atlas, the foramen for the

<sup>1</sup> Cleland, *Nat. Hist. Review*, April 1861.

<sup>2</sup> Allan, *Journ. Anat. and Phys.* vol. xiv. p. 18.

vertebral artery and the inferior articular surfaces conform to the normal on both sides. The posterior surface of the anterior arch presents a well-marked facet for articulation with the odontoid process. The left hypoglossal canal is in the form of two separate compartments separated by a bony partition 2 mm. thick.

*Specimen II.* In fig. 1 is represented another specimen, not unlike the preceding, in which the atlas is adherent to the occipital. Here, the occipital condyles are fused with the superior articular processes of the atlas, the fusion being most complete laterally. On the right side a narrow fissure passes medio-laterally between the fused processes. This on careful examination shows the articular surface of the occipital condyle. The line of fusion on both sides is clearly indicated by a sulcus.

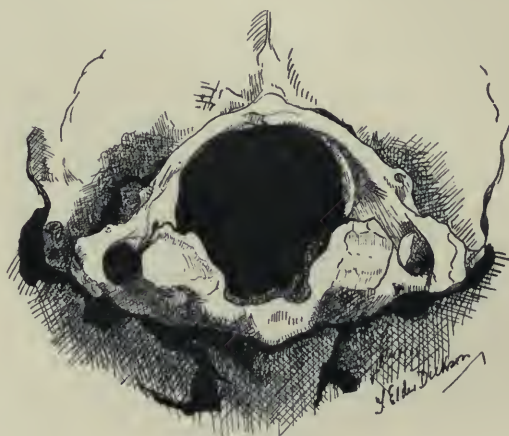


Fig. 1

The anterior arch of the atlas is not so strongly developed as in the previous specimen, but its upper border is separated from the anterior margin of the foramen magnum by an irregularly oval interval measuring 15 mm. broad by 8 mm. deep. The facet for articulation with the odontoid process is poorly marked and this is partly explained by the fact that the inferior articular surfaces are small and show indications of having been partially fused to the axis. The transverse process is normal on both sides and as usual the anterior and posterior tubercles are not well developed.

The posterior arch of the atlas is thin and poorly developed. The upper margin of the arch is fused posteriorly with the posterior margin of the foramen magnum. This is a further stage of fusion than that described by Allan in which small articular facets are developed between the posterior arch and the posterior margin of the foramen magnum. On the right side the sulcus for the vertebral artery is converted into a canal.

The jugular processes of the occipital bone are well developed on both sides while at its lateral extremity each has an irregular tubercle almost as large as the lateral extremity of the transverse process of the atlas. This tubercle

extends downwards for a few millimetres and is separated from the occipital condyle by a well-marked fossa. It is to be noted that the margin of this fossa in the region of the foramen magnum is strengthened, having the appearance of a distinct ridge. The hypoglossal canals have their normal position and appearance.

*Specimen III.* In fig. 2 the fusion has proceeded a stage further than in the preceding specimens. On the right side the occipital condyles and the lateral mass of the atlas have fused into a solid mass. On the left side the fusion, though complete, still shows traces of a previous articulation in the form of a shallow sulcus. The anterior arch is very strongly developed as is also its anterior tubercle but the upper border of the arch is separated from the anterior margin of the foramen magnum by an interval of less than 2 mm. On the right side ossification has extended anteriorly between the atlas and occipital bone for a few millimetres from the occipital condyle.



Fig. 2

The articular facet for the odontoid process is much larger and better developed than normally, whilst the transverse ligament which stretches between the lateral masses of the atlas, and retains the odontoid process in position is ossified and in the form of a thin bony plate, a condition found not uncommonly in birds.

The transverse processes are poorly developed especially the costal element which is present merely as a thin spicule of bone completing the transverse foramen. The lateral extremities of the transverse processes do not show differentiation into anterior and posterior tubercles.

The posterior arch of the atlas exhibits a wider range of variation. The arch is deficient behind, the extremities of the laminae failing to meet by a distance of 8 mm. The right lamina is the shorter and is fused along its whole length to the occipital bone, leaving only a canal for the vertebral artery to enter the cranium. This canal is not formed merely by the development of the superior oblique process already referred to, but is placed between the occipital bone and the posterior arch of the atlas. The inferior aspect of the right side



of the arch measures 1 cm. at its widest, that is, immediately underlying the canal for the vertebral artery, and is perforated by a foramen 2 mm. in diameter which probably transmitted a communicating branch between the first and second cervical nerves. The left half of the posterior arch of the atlas stands out freely from the posterior border of the foramen magnum, being separated from the occipital at its nearest point by a distance of 4 mm. The posterior extremity is slightly rounded.

The jugular fossa on the left side is decidedly larger than normal and opening into the fossa is the posterior condyloid canal. The left hypoglossal canal is smaller than normally and anteriorly is separated from the jugular foramen by a very thin plate of bone. The right hypoglossal canal is normal in all respects.

*Specimen IV.* In the next specimen (fig. 3) the condition is somewhat similar to the preceding except that the fusion is more complete on the left side.



Fig 3

The anterior arch is strongly developed and presents a well-marked tubercle. The anterior atlanto-occipital interval measures 4 mm. at its greatest vertical diameter, and is 13 mm. broad. There is also a prominent articular facet for the odontoid process. On both sides the superior articular facets of the atlas are fused with the occipital bone but on the right side there are still traces of the line of demarcation. The transverse processes are complete on both sides with a foramen for the vertebral artery. Both the costal and transverse elements are diminished in size and on each side the transverse process is in contact with, although not fused to, a small paracondyloid process. The atlas before becoming fixed in position appears to have been rotated anteriorly on the right side round an axis whose centre was near the left superior articular process, so that the lateral margin of the right transverse process came into

contact with the postero-medial margin of the styloid process and thereafter became fused to the latter process.

The posterior arch of the atlas is deficient posteriorly, the free extremities of the laminae being separated by a distance of 7 mm. On the left side the arch is entirely assimilated into the margin of the foramen magnum and only the lower border of the posterior extremity of the lamina is prominent. There is a complete bony tunnel 1 cm. long for the vertebral artery, between the occipital bone above and the posterior arch of the atlas below. On the right side the lamina is free in its whole extent and well developed. The interval between the foramen magnum and the arch for the passage of the vertebral artery is diminished in size and a tiny spicule of bone projects from the upper and inner border of the lamina which in the recent state probably gave attachment to the fibres which constitute the arch over the vertebral artery.

Between the paracondyloid and condyloid processes there is a deep fossa which causes the margin of the foramen magnum to stand out prominently on the right side.

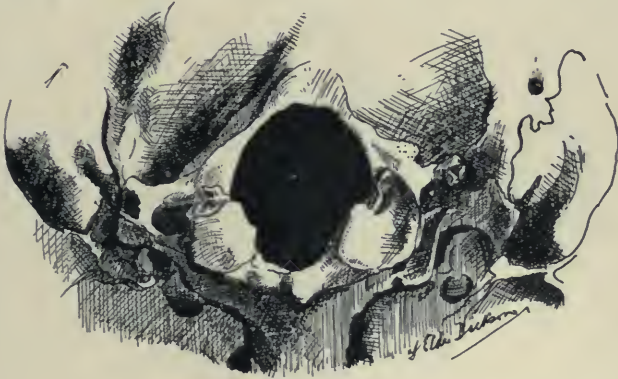


Fig. 4

The inferior articular surfaces of the atlas, however, show remarkable variation. On the left side, that is, the side of most complete assimilation of the posterior arch, the facet is concave transversely and very slightly convex antero-posteriorly, while on the right side, which is least assimilated, the facet is convex in all directions, a point of considerable importance in connection with Kollmann's definitions for manifestation of occipital vertebrae.

From the description of the two preceding specimens it is obvious that the atlas may be assimilated obliquely into the skull base.

*Specimen V.* In fig. 4 I have illustrated a further stage towards assimilation of the atlas. In this specimen the anterior atlanto-occipital interval is almost obliterated, leaving only a small cleft 5 mm. long, slightly to the left of the middle line. The anterior arch is well developed with a normal anterior tubercle and facet for the odontoid process. The superior articular process of the atlas is fused to the occipital on both sides. On the right side there is no trace of

the joint cleft, but on the left side the cleft is indicated antero-laterally by a faint groove leading from the lateral margin of the anterior atlanto-occipital interval.

The transverse processes are complete and relatively small. The foramen for the vertebral artery is present on both sides and the processes are entirely free from the occipital bone. The posterior arch, however, is entirely assimilated into the foramen magnum causing the posterior rim of that opening to stand out prominently. Where the laminae meet posteriorly the surface is flattened out and roughened. Between the occipital bone and the laminae is the canal by which the vertebral artery entered the cranium. On the right side there is also a small canal, commencing at the posterior margin of the transverse process and formed between the lateral margin of the assimilated arch of the atlas and the occipital bone which probably lodged the posterior division of the suboccipital nerve. Passing from the anterior margin of the external orifice of the vertebral canal is a deep groove which ends at the hypoglossal canal, and probably conveyed the anterior division of the suboccipital nerve



Fig. 5

to the hypoglossal nerve. Since the muscles of the first neck segment must have been absent the nerve was probably distributed to the musculature of the tongue.

In this specimen also the inferior articular surfaces are of interest. On the right side the facet is almost circular and is convex corresponding to an occipital condyle, while on the left side the facet is reniform in outline, smaller than an occipital condyle, yet larger than an inferior atlantal surface. The surface, however, is almost flat. The assimilation in this case is more complete on the left side than on the right.

*Specimen VI.* In the specimen illustrated in fig. 5 the anterior arch is small and poorly developed. The anterior tubercle is well marked, but the facet for the odontoid process is relatively small, although it is quite distinct. The lateral masses of the atlas are fused to the occipital bone and a small triangular median anterior atlanto-occipital interval is present. On the left side the transverse process is complete but slightly developed and contains



the foramen for the vertebral artery. Its lateral extremity is fused to a short paracondyloid process forming an antero-posterior canal between the occipital bone and the transverse process. On the right side the transverse process is slightly better developed and is also complete. It is, however, entirely free from the occiput.

The posterior arch is more completely absorbed into the occipital than in the previous specimen and there is no trace posteriorly of the fusion. Laterally, more marked on the right than on the left side, there is a deep groove, the lateral sulcus, which probably transmitted the posterior division of the suboccipital nerve and this groove makes the lateral margin of the lamina more prominent. The inferior articular facets are not so obliquely set as in the normal atlas and both are slightly convex, the right facet showing a tendency to elongation.

*Specimen VII.* Fig. 6 shows yet another specimen in which the process of assimilation is still more advanced. Here, the anterior arch of the atlas is



Fig. 6

quite distinguishable with a small anterior tubercle. The facet for the odontoid process is very small and represented by an area 2 mm. in diameter. The lateral masses and the upper border of the anterior arch of the atlas are fused to the occipital bone, leaving only a small central foramen 1 mm. in diameter as the representative of the anterior atlanto-occipital interval. There is no evidence of the dividing line save for a faint sulcus passing a short distance laterally from this central foramen.

The hypoglossal canal appears at first sight to present a double orifice on the external aspect, but on closer examination the lower and more external of the two is found to be continuous with a separate canal having an internal orifice on the inner aspect of the lateral mass of the assimilated atlas, that on the right side being separated from the internal orifice of the hypoglossal canal by a distance of 7 mm. and on the left side by 3 mm. This lower canal presumably conveyed the first cervical nerve.

The left transverse process is still distinguishable, the transverse element being more superior at its lateral extremity as in the normal atlas, and is fused to a small paracondyloid process, while the costal element is represented by a thin spicule of bone. This spicule being attached internally and in front to the lateral mass, and externally to the transverse element, encloses a small foramen which, however, on account of its size cannot have conveyed the vertebral artery. On the right side the transverse process is represented only by a small tubercle of bone without any definite characteristics.

The posterior arch of the atlas is entirely absorbed into the occipital with only a suggestion on the left side of its presence near the lateral mass, the free lateral margin being brought into relief by a shallow fossa on the occipital bone.

Concerning the inferior articular processes it is again to be noted that on the right side, which gives indications of greater assimilation, the facet is concave while on the left side the surface is slightly convex. On both sides it corresponds in outline with the inferior articular facet of a normal atlas.

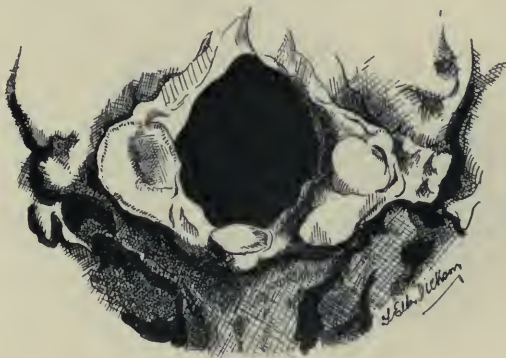


Fig. 7

*Specimen VIII.* Fig. 7 illustrates a most interesting specimen. On the right side of the occipital bone there is a typical occipital condyle with its long axis directed from before backwards and outwards. It is convex in its long axis, the surface being directed downwards, outwards and slightly backwards, corresponding in all its details with the normal occipital condyle. On the left side the condyle is similar in outline to the inferior atlantal surface but somewhat larger, measuring 2.2 cm. in its long axis and 1.8 transversely, compared to the normal average of 2 cm. by 1.5 cm. The left surface is marked by a groove slightly convex outwards dividing it into almost equal parts, a medial convex part and a lateral concave part. The anterior margin of the foramen magnum is thickened in the form of an anterior arch extending forwards on each side from the anterior extremities of the masses which support the articular surfaces. Anteriorly the arch presents a well-marked tubercle and on its posterior or internal aspect there is a circular articular facet 1 cm. in diameter, concave in all directions. The axis perpendicular to this facet if

prolonged anteriorly would strike the nasion, the surface facing downwards and backwards. This facet could only have been for articulation with the odontoid or some such similar process. Projecting laterally on each side from the bony mass supporting the articular surface is an irregular ridge of bone having a bifid free extremity near the occipito-mastoid suture, giving the indication of the formation of a transverse process.

Between the pharyngeal tubercle and the tubercle on the anterior arch is a deep groove, *sulcus anticus*, passing laterally and ending at the hypoglossal fossa which on the left side is distinctly larger than normal. Externally each hypoglossal fossa presents a double foramen. The upper and more medial is continuous with the hypoglossal canal proper while the lower passes downwards, inwards and backwards, to open internally near the centre of the lateral mass of bone supporting the articular surfaces. It probably conveyed the first cervical nerve. As the muscles of the first segment must have been

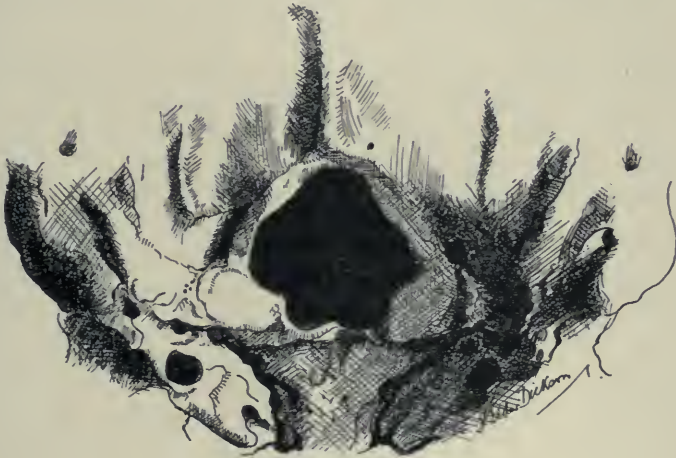


Fig. 8

absent, one may suppose that the nerve of the segment joined the hypoglossal nerve and was distributed to the tongue musculature and infrahyoid muscles.

The posterior margin of the foramen magnum is normal in appearance, but laterally the margins are thickened giving the indications of laminae, the lateral margins of the laminae being undermined by a rough irregular groove. The mass of bone supporting the articular facet which approximates to the occipital is almost twice as deep at the margin of the foramen magnum as the bony mass supporting the atlantal facet.

*Specimen IX.* At first sight the next specimen (fig. 8) gives the impression of "manifestation of an Occipital Vertebra." The occipital condyles have the direction of the normal condyles but the articular surfaces are perfectly flat, while the right condyle has a ridge 2 mm. deep on its lateral aspect at right angles to the articular surface, just as if the condyle had been worn down by constant friction.



The posterior margin of the foramen magnum is raised into a ridge, more marked on the left side, simulating the lamina of a vertebra and corresponding to the post-condyloid process of Mannu. The ridges when traced posteriorly are found to merge into a crest which extends posteriorly in the median plane for a distance of 2.5 cm. from the posterior margin of the foramen magnum. This crest simulates the spinous process of a vertebra and on each side of it is a shallow fossa which makes the ridge appear more prominent.

The anterior margin of the foramen magnum is very thin and irregular. The basisphenoid and basioccipital are fused, but the base of the skull is so depressed that this part lies parallel to Reid's base line. The hypoglossal canal has also suffered from the pressure and on the right side its intra-cranial orifice is represented by a very narrow transverse fissure. This orifice is so small that one must conclude that the subject must have suffered from paralysis of the corresponding side of the tongue, unless the fibres were conveyed by another route. The left hypoglossal canal is more nearly normal, but it also is slightly flattened from above down.

The specimens which I have described are drawn from a collection of nearly 800 skulls belonging to the Anatomical Department of Glasgow University, and as those under consideration number nine, this gives slightly more than 1 per cent. variation in the cranio-vertebral region. As has been shown, the tendency in variation is chiefly in the direction of reduction in the posterior arch of the atlas and this fact is also verified clinically by the comparative frequency of spina bifida. The first six specimens I have described are undoubtedly phases in the progression of assimilation of the atlas and it is therefore only the last three which are at all controversial, thus giving 0.4 per cent. of cases showing marked divergence from the normal condition of the skull base.

Various rules have been laid down for determining whether the condition is one of "assimilation" or of "manifestation." Kollmann maintained that the shape and curvature of the articular surfaces indicate the nature of the case, yet as I have shown in fig. 3 the articular surfaces are in this specimen tending to take on the characteristics of an occipital condyle, and this change is most marked on the side on which assimilation is most complete. In the instance illustrated in fig. 4 the articular surfaces tend still more towards the form of the occipital condyle and the specimen illustrated in fig. 5 has similar characteristics. It is fairly obvious, then, that one cannot dogmatise on the shape and curvature of the condyles. Professor Elliot Smith also, by his specimens, exhibited to the Anatomical Society in 1908, proved that this theory could no longer be accepted. Professor Cleland has shown that throughout life the length and degree of curvature of the condyles vary according to the age of the individual, and to the secondary curves of the spinal axis, in order that the proper balance of the skull on the vertebral column may be maintained. We are therefore justified in concluding that the shape and curvature of the condyles is primarily determined by functional factors, to

admit of flexion and extension of the skull. That there is a functional significance in the variations to be seen in the occipito-atlantal articulation is indicated by the fact that in the Simiidae in which the foramen magnum is relatively far back, one can trace the reduction of the posterior extremities of the occipital condyles from the lowest to the highest as the anthropoids tend to assume the erect attitude. Flexion and extension, as is well known, occur in the other moveable regions of the spine by compression and relaxation of the intervertebral disc which is absent between the atlas and the occiput and therefore the articular surfaces are modified to compensate for this factor. We might therefore expect that if the atlanto-occipital articulation is ankylosed the succeeding articulation would become modified, given sufficient time, to permit of the required movement. It is also obvious that if the spine of the vertebra is present, or even the laminae, the amount of nodding movement at the atlanto-axial articulation will be limited, the remainder being accomplished through the medium of the intervertebral discs of succeeding vertebrae. That vertebrae can be modified to resemble preceding or succeeding vertebrae is amply demonstrated in the lower regions of the column. There seems no reason why the succeeding articulation should not take on the saddle-shaped surfaces characteristic of the atlanto-occipital articulation. Moreover, the curvature of this articulation varies with age. In the birds where the neck region shows very great flexibility the articulations between the centra of the cervical vertebrae are nearly all of the saddle-shaped variety. At the other extreme are the Cetaceans in which the neck is relatively short and thick, and movement is almost lost, and the cervical vertebrae are frequently fused into a solid mass. No one would suggest that this latter condition is a developmental error, but merely a failure on the part of Nature to perform unnecessary work. In other mammals there is only one saddle-shaped articulation on each side between the atlas and occiput, and the articular surfaces of the other cervical vertebrae have become flattened. This allows the maximum amount of rotation which, in the neck region, is not limited as in the thoracic region, by costal processes.

Swjetschnikow states that absence of the atlanto-occipital interval, together with absence of foramina transversaria and sulcus for vertebral artery indicate "manifestation of occipital vertebra," yet Professor Elliot Smith has shown that all those conditions may be satisfied even in a case of undoubted assimilation of the atlas.

In fig. 6 I have illustrated a case very similar to one described by Professor Elliot Smith in which the canal for the suboccipital nerve opens anteriorly with the hypoglossal canal, with the exception that, in the specimen I have described, the skull was perfectly normal in all features except in the region of the foramen magnum, whereas in Professor Smith's case the whole skull was abnormal.

The specimen shown in fig. 7 is more difficult to place. The third condyle which is present is obviously an articular surface for the odontoid process and is not formed by any prolongation of the articular surfaces on the lateral



masses. Here, then, is a case which, according to Kollmann, from the shape of the condyles must, on one side, be a manifestation of an occipital vertebra and on the other side assimilation of the atlas. Again, from Swjetschnikow's formula, in having neither anterior atlanto-occipital interval, foramen in transverse process, nor sulcus for vertebral artery it should be diagnosed as an occipital vertebra, yet this assumption is negated by the very presence of the third or median condyle in its particular form, and by the presence of the canal for the suboccipital nerve running into the hypoglossal canal. The latter condition is similar to that in the preceding case, and resembles the case described by Professor Elliot Smith. Considering all these factors this abnormality is stamped as an extremely high grade of assimilation of the atlas, and represents a more advanced stage than the Edinburgh case described by Professor Cunningham and Professor Kollmann.

With regard to the dog's skull figured by Professor Kollmann a few remarks may be appropriate. It is stated that on the left side there is an occipital condyle and on the right side a half atlas with an inferior atlantal articular surface. Extending between the two articular processes is an irregular articular surface which Kollmann has differentiated dogmatically into two parts. The left half, he considers, is a third hemicondyle and the right is the medial part of the inferior surface of the atlas. From careful examination of his figure and of the text I fail to see an exact dividing line which could differentiate one half as being first cervical segment while the other half is occipital segment, and I would suggest that this is a case of oblique assimilation of the atlas similar to the human specimen which I have described and illustrated in fig. 7. In this dog's skull the left part of the atlas has been entirely assimilated into the skull base with modification of its inferior articular surface to resemble an occipital condyle. The right side of the atlas has not been so completely taken up and shows all the characters of a neck vertebra. In the various specimens I have described not one indicates an exactly horizontal assimilation, but always one side is more involved than the other. Neither can one say that either side is particularly liable to variation as the specimens are very evenly divided.

When or how this assimilation has occurred is difficult to say; yet in the more complete forms of assimilation the elements must have fused at a very early stage of development. It is now well known that the ovum becomes embedded in the uterine mucosa and it is extremely doubtful whether pressure could produce an alteration at this stage (Schiffner's *Drucktheorie*). It seems more probable that it is a fault in the arrangement of the parts which, as we know, leads to so many abnormalities in other tissues.

With regard to the lesser forms of fusion of the atlas it is conceivable that abnormal intrauterine pressure may produce the condition under consideration. Yet, again, pressure in a fluid is essentially equally distributed and therefore the abnormality could only be produced if there were a deficiency of liquor amnii or if the amniotic cavity were divided into loculi by abnormal adhesions. In either case there is evidence of more superficial damage in the



form of adhesions and although in dealing with dried specimens one does not know the external form of the subject, still, it is reasonable to suppose that any pressure which was great enough to induce fusion of neck vertebrae would be sufficiently great to produce evident deformities of other parts and probably also of the brain capsule. This also points to the cause of assimilation being intrinsic, not extrinsic.

With reference to the depressed skull shown in fig. 8, some points are of importance. I do not believe that the appearance of the skull base amounts to a manifestation of an occipital vertebra, although it may suggest the vertebral origin of the occipital. As has been indicated the posterior arch of the vertebra is the first to disappear and this is true for all regions of the vertebral axis. It is only right to expect then, that the posterior arch would be the last to reappear in a regressive condition as a manifestation of an occipital vertebra. Yet in this specimen the posterior margin of the foramen magnum is very



Fig. 9

strongly developed while the anterior margin is extremely thin and irregular. Then again the hypoglossal canal does not show any abnormality in the direction of indicating its plural character as one might reasonably expect in a regressive condition and as this feature is indicated in the progressive conditions of assimilation just described.

We must conclude therefore that the thickening of the margin of the foramen magnum and the production of the spine posteriorly are secondary physiological characters produced to compensate for the loss of stability created by the depression of the skull base.

That articular surfaces are an unreliable guide to diagnosing abnormal phenomena is indicated by the frequency with which the posterior margin of the foramen magnum shows articular surfaces for articulation with the upper border of the posterior arch of the atlas, and the formation of new joint cavities in dislocations. In a skull (fig. 9) in the possession of the

Anatomical Department and figured by Dr Rankin<sup>1</sup> there is a remarkable development of what he called "adventitious condyles." This skull is particularly massive and the subject before death was an imbecile in whom movement of the head was extremely slow and limited. On either side of, and posterior to, the occipital condyles are developed two reniform articular surfaces, the long axis being in the reverse direction to that of the occipital condyles, that is, backwards and inwards. Each is separated from the corresponding occipital condyle by a groove so that the articular surfaces are not continuous. The surfaces are flattened with a tendency to concavity. From the position of these surfaces it seems fairly certain, in the light of our present knowledge, that the additional articular facets articulated with the transverse processes of the atlas by the development of processes (*processus supratransversarii*) similar to those which fuse with the paracondyloid processes as previously described and that, in fact, the articular surfaces are carried on short paracondyloid processes.

No one questions the fact that the occipital bone is the product of one or more spinal segments, and skulls frequently give indications of the vertebral origin of the occipital region by the presence of such bony formations as a posterior arch, posterior tubercle representing a spinous process, third condyle (but I suggest only in those cases in which the dens of the axis is particularly long and articulates with the anterior margin of the foramen magnum), condyloid tubercle, sulcus ambiens between the pharyngeal tubercle and the anterior border of foramen magnum, and sulcus lateralis. I believe, however, that when the abnormality is such that an additional vertebra is indicated, the case is always one of assimilation of an atlas as the series I have described shows, never of a throwing-out of an occipital vertebra.

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<sup>1</sup> *Edinburgh Monthly Journal of Medical Science*, 1843, p. 1071.

# A SYSTEM OF TUBULES IN SECRETING EPITHELIA<sup>1</sup>

## PRELIMINARY NOTE

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THE purpose of this note is to call attention to the existence of a new structure distributed through the parenchyma of certain secreting epithelia. The structure consists of an extensive system of minute tubules linked together in the form of a network, which is stretched beneath the free surface of the epithelia.

It is here described in the secreting epithelium of the thyroid gland, because it occurs as a peculiarly isolated structure in the parenchyma of this gland. It must, however, be understood that the general description given is equally applicable to the structure as it occurs in other secreting epithelia—certain portions of the kidney tubules, bile ducts, etc.—though in these cases and in others its relationships are complicated by the existence of factors not present in the thyroid gland.

The local distribution of the system in the human body, and its comparative anatomy, have not yet been worked out.

The successful demonstration of the structure depends largely on the employment of a special technique detailed in this paper. It is essential to use for examination fresh tissue soon after removal from the body: post-mortem changes are peculiarly apt to disintegrate the structures.

## HISTOLOGICAL TECHNIQUE

This is essentially an elaboration of the Zenker and phosphotungstic-acid-haematoxylin method devised by Mallory for neuroglia and fibroglia fibrils. The modification introduced is the use of a special fixing agent, which at the same time as fixing, appears to have a mordanting action on the impregnated tissues. This fixing and hardening mordant—for convenience termed F.B.C. fluid—is made as follows:—

Potassium bichromate, 40 grms.; chromium fluoride (fluorchrom), 40 grms.; distilled water, 2000 c.c. To dissolve, boil for half an hour; cool thoroughly and filter. To the filtrate add: corrosive sublimate, 100 grms. To dissolve, boil for half an hour; cool thoroughly and filter.

Pieces of tissue, not exceeding 3 mm. thick are thoroughly fixed, hardened and mordanted in 12 hours. It is necessary to wash in running water for not less than 12 hours before the tissue is taken on to paraffin, celloidin or gum.

<sup>1</sup> The expenses of this research were in part defrayed by a Grant from the Medical Research Council.



If the fluid is used as a simple mordant after formalin, alcohol or osmic acid, etc., washing is essential before immersion. It should be noted, however, that acetic acid, formic acid and other agents generally credited with augmenting penetration are inimical to the effect of this mordant.

The staining process used in this laboratory differs only in slight details from that used by Mallory<sup>1</sup> and is as follows:—

1. Xylol: absolute alcohol.
2.  $\frac{1}{2}$  per cent. alcoholic iodine: 10 minutes to remove the mercurial precipitate. (It seems to possess some other virtue than this and is essential to the process.)
3. 95 per cent. alcohol:  $\frac{1}{2}$  hour.
4. Clean alcohol: water.
5.  $\frac{1}{4}$  per cent. aqueous solution of potassium permanganate, 10 minutes: water.
6. 5 per cent. aqueous solution of oxalic acid until just decolorised.
7. Running water, 10 minutes.
8. Phosphotungstic-acid-haematoxylin, 15–24 hours.

After this staining process the section should very rapidly be washed in alcohol, cleared in xylol, and mounted in xylol-balsam or other medium.

The polychromatic differentiation so obtained of the various structures in the tissue is remarkable in daylight, but ordinary artificial light cannot be used. The differentiation in tone, however, is clearly visible with light of wave length 5100–6200 A.U. (Wratten “M” screens B and C).

The staining technique is worthy of very general adoption, since it gives a high degree of differentiation of tissue, but in this note attention is confined to the intraparenchymatous tubular system which it has revealed. The stain has no keeping qualities.

We have to acknowledge our indebtedness to Miss H. M. Cunningham, B.Sc. for her valuable assistance in elaborating this technique.

#### THE SYSTEM OF TUBULES IN THE THYROID GLAND

The secreting epithelium of the thyroid gland appears as the lining epithelium of its characteristic follicles. The epithelium is described as both cubical and columnar, or, in other words, there is a variable depth of coarse cytoplasm, between the peripherally disposed nuclei and the contents of the follicle.

In a segmental section of the follicles this zone of cytoplasm contains short rods and dots of darkly stained material, having the appearance of a fence between the nuclei and the colloid substance within the vesicle (fig. 2). These rods and dots may alternate regularly, but more often the line of the fence is broken. This fence of rods and dots is separated from the contents of the follicle by a layer of cytoplasm which is always present no matter what the degree of distension of the follicle.

<sup>1</sup> Mallory and Wright, *Pathological Technique*, 7th edition, 1918, p. 149.

Follicles may be cut in such a way as to leave a roof of cytoplasm only over the colloid, or, on the other hand so as to permit a floor of epithelium to come into view through a thin layer of colloid. Under these circumstances the rods are seen to be the boundaries of the open mesh of a network, and the dots to be nodes formed by the junction of these rods. The mesh so formed is roughly polygonal.

It is apparent, particularly in thick sections, that the network occupies a plane of its own distinct from the plane of the nuclei. Occasionally the plane of section passes between the nuclei and the tubules, leaving the network exposed, and showing the mesh filled with granular cytoplasm.

The parenchyma of the thyroid gland is not infrequently devoid of vesicles, as is the case in the foetal gland, and in many areas of normal thyroid glands. In this absence of vesiculated colloid, the central zone of cytoplasm of the follicle is occupied by the system of tubules (fig. 3). When such a follicle is

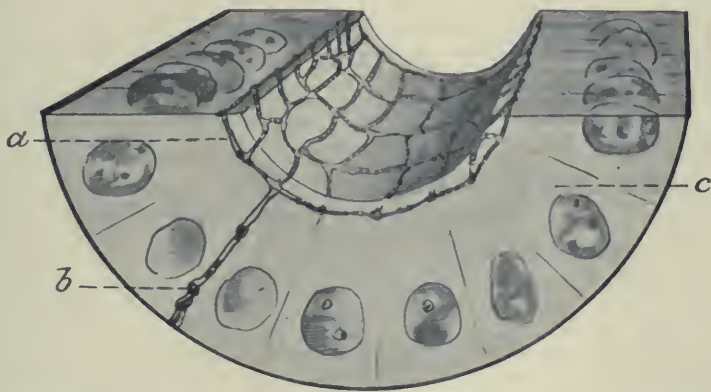


Fig. 1. Schematic drawing of a secreting epithelium showing the position of the tubular network: (a) tubular network; (b) very occasional radial branch; (c) cytomitome.

cut in length the system has the appearance of a loosely hanging seine, the mesh of which is partially collapsed. In cross-section of such a follicle the system appears in the central zone of the cytoplasm as a ring or rings of chromatic material. Occasionally a nodal point suggests a signet ring. Where two or more rings appear, as may be the case, they are obviously linked together and occupy different planes in the depths of the section.

From this condition of extreme collapse to the fully extended condition of the mesh in the vesicular follicle, every degree of stretching can be seen. Whatever the degree of stretching or collapse, however, the system of tubules occupies that precise position in the cytoplasm that has already been made out in the vesicular gland; that is to say wherever there is contained material in the gland parenchyma, this system of tubes subtends it, but is always separated from it by a layer of cytoplasm (fig. 1).

The system extends over a wide area of epithelium; it is not a structure

pertaining to a single cell, but has a continuity in the parenchyma limited rather by the area of a functional unit than a cellular one.

Emphasis has been laid on the fact that this system of tubules occupies in the cytoplasm, a specific plane orientated about the centre of the follicle. On rare occasions, a section will reveal a branch running radially from the network towards the base of the epithelium (figs. 1, 3). Such branches are always solitary, very infrequent and usually larger in calibre than the tubes enclosing the mesh of the network.

The features already outlined represent the variations in appearance of the system of tubules as a system. Other appearances depend upon alterations occurring in the component tubules. These latter concur with the rest-phase and the active phase of the epithelium in which the system is set.

In the rest-phase of the epithelium the tubes appear as thin, solid, homogeneous structures, having a diameter of  $0.2\mu$  to  $0.5\mu$ . They stain opaque purple or black. In the active phase this no longer pertains; they increase markedly in their diameter to as much as  $2\mu$ ; they lose their solidity and appear as hollow structures. Their walls now stain a pale lilac colour and are transparent. The content of the tubule is either a clear homogeneous material, or a granular material (figs. 4, 5). The granules are discrete and densely chromatic, and frequently give the tube a beaded appearance (fig. 5). The staining affinities of the granules are identical with those of the granules of the cytoplasm. Occasionally a tube cut in cross-section shows a dark granule, enclosed in a pale lilac-stained wall.

## DISCUSSION

The structural appearances outlined in the foregoing description cannot be artefacts since they are demonstrable in every thyroid gland, normal and pathological. They have a precise distribution and position, a very uniform size and shape, and they vary directly with the state of physiological activity of the epithelium in which they lie.

The intraparenchymatous system described has a definite disposition in relation to the cells of the epithelium. It is not to be confused therefore with the intracytoplasmic filaments of the cytomitome: nor with the intracytoplasmic canaliculi of Holmgren, D'Agata, the reticular material of Cowdry<sup>1</sup> and others; nor with so-called paranuclear structures, mitochondria, etc. On the other hand its position in the parenchyma is much the same as the marginal chromatic centriole of columnar epithelium, the basal particles of ciliated epithelium and the isotropic material of Englemann.

These structures, however, are described as confined to individual cells; it may be that the description of them depends upon the failure of technique to demonstrate them in their continuity<sup>2</sup>. This last probability is under investigation.

<sup>1</sup> E. V. Cowdry, *Amer. Journ. Anat.* Vol. xxx. No. I, Jan. 1922.

<sup>2</sup> Pensa. Quoted by Da Fano, *Journ. of Physiol.* Vol. lvi, No. 6, Oct. 1922, p. 461.



For a long time before perfection of the staining technique, a doubt remained as to whether the appearances could be due to the cut edge of cell-membranes. This possibility is not to be entertained for the following reasons:

The structures have never been seen to run in the protoplasm from the centre to the periphery of the parenchyma, enclosing the cell at its margin, as must be expected were a cell-membrane in question. The components of the network are never internuclear in position, and appear only in certain planes in the cytoplasm. It is frequently necessary to focus through the depth of the protoplasm before the network becomes visible; or the network will have long passed out of focus before an adjoining nucleus is seen. Lastly, fragments of the network are often found lying free in vacuoles within the protoplasm.

It is clear, then, the structures are not cell-membranes.

It is impossible to doubt the tubular nature of these structures if a comparison is made between their appearance in resting and active epithelium. Further, a comparison with other tubular structures—the bile canaliculi of the liver—places the matter beyond doubt. This new structure and the bile canaliculi occur as a network; they are both at times seen as dots and bars; both alter with the particular phase of activity of the associated parenchyma. When empty they are thin, homogeneous, darkly staining lines; when full they are pale membranous structures enclosing differentially stained matter or highly granular material. Indeed these two structures seem to differ only in calibre and in size.

On the whole there is every justification for considering the structures described in this paper as a specific system of tubules peculiarly arranged in the parenchyma of certain secreting epithelia.

It should be stated that these tubules can be seen but faintly, with stains other than the special stain used in this research.

No definite knowledge is claimed of the significance and function of this intraparenchymatous tubular system; the matter is under investigation in this laboratory.

One significance that could be attached to these structures is that they function as an auxiliary circulation carrying lymph, blood-plasma, peculiar contents of parenchyma, or the contents of gland-ducts.

To find so delicate a structure brought into such close approximation to the superficial surface of secreting membranes could point to some special function to do with secretion or absorption.

The lumen of the tubules is so fine—not exceeding  $2\mu$  at its maximum—as to preclude the possibility of any association with a circulation maintained by mere mechanical pressure. Flow in such tubules would depend upon some biodynamic factor—and this opens up a field of many new and significant possibilities which might provide a key to some of the more pressing problems of the moment connected with excretion and absorption.

## SUMMARY

1. A system of intraparenchymatous structures is described in the secreting epithelium of the thyroid gland.

2. This system consists of a network of tubules stretched beneath the free surface of the epithelium.

3. Very occasional radial branches from the system pass towards the base of the epithelium.

4. When secretory activity is obvious in the parenchyma these tubules are distended and contain granular material.

5. The structure is described in the thyroid gland, but occurs in other secreting epithelia.

## DESCRIPTION OF PLATE

Fig. 2. Section of thyroid gland showing the position of the tubular network: (a) dots and bars concentrically arranged within the epithelium; (b) network of tubules.

Fig. 3. Section of thyroid gland showing various appearances of the tubular system in follicular and interfollicular tissue. Note (a) radial branch running the depth of the parenchyma.

Fig. 4. Section of the thyroid gland showing the "hanging seine" effect of the partially open mesh. Note the broken granular content of the tubes.

Fig. 5. Section of the thyroid gland showing tubular network during period of activity of the gland. Note (1) the tubular nature of the structure; (2) the granules within the tubules.

NOTE. The microphotographs are untouched photographs.

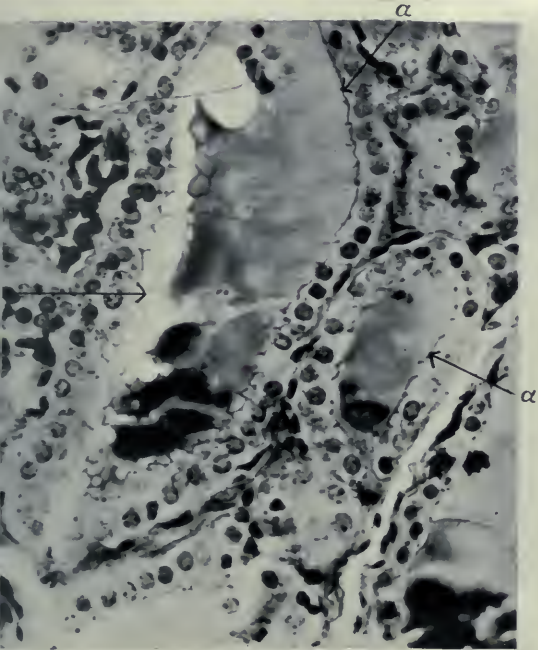


Fig.2

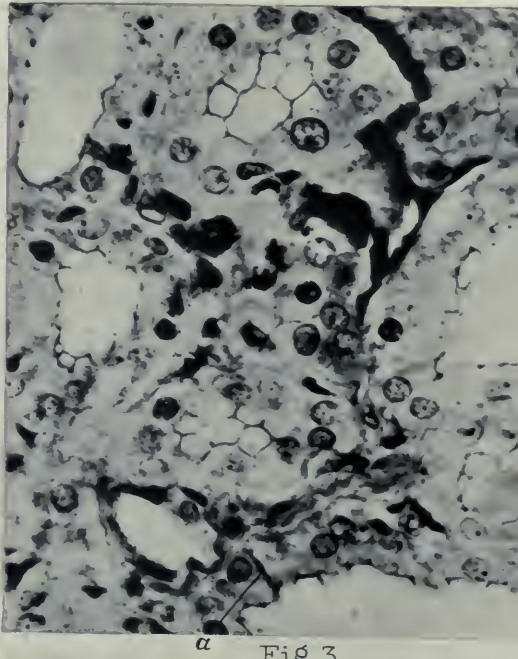


Fig.3

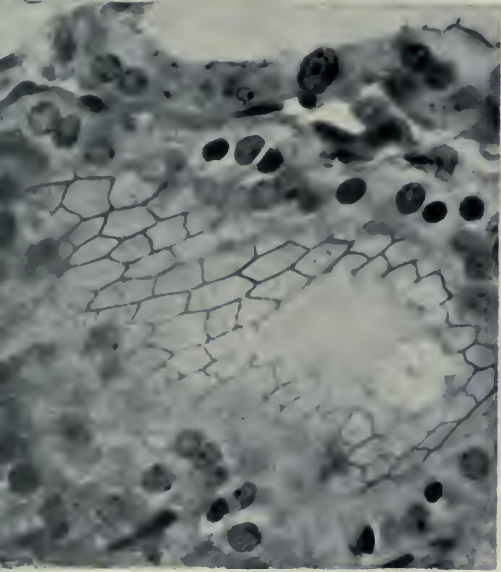


Fig.4

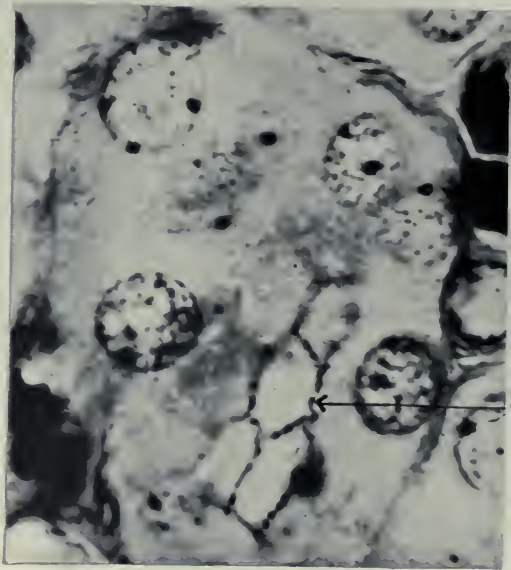


Fig.5





## THE ANATOMY OF SO-CALLED DEEP SENSIBILITY

BY JOHN S. B. STOPFORD, M.D.

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AT the present time it is customary to divide the loss of sensation, resulting from the section of any nerve containing sensory fibres, into cutaneous (epicritic and protopathic) and deep. This division was suggested by Head as a result of his investigations of patients suffering from division of a peripheral nerve and the observations made in a "Human experiment in nerve division." Our knowledge of deep sensibility is based almost entirely upon a study of the residual sensation found in Head's own hand after section of the radial nerve at its origin from the musculo-spiral, and of the musculo-cutaneous at the point where it perforated the deep fascia, just proximal to its division into the two branches which supply respectively the anterior and posterior aspects of the pre-axial half of the forearm. These nerves were selected because it was believed that, since they are usually described as having a purely cutaneous distribution, a fairly large area of skin would be rendered completely insensitive and yet the sensibility of the subcutaneous tissues would remain undisturbed. From an examination of the residual sensation it was stated that "deep sensibility" was capable of responding to pressure, passive movement of joints and pain caused by excessive pressure. It was also stated that a part endowed only with deep sensibility possessed not only the power of recognising the stimulus but also the power of localising a pressure stimulus with remarkable accuracy. Furthermore it was decided that "the fibres subserving this form of sensation run mainly with the motor nerves, and are not destroyed by division of all the sensory nerves to the skin." From the foregoing it will be realised that the division of sensation into cutaneous and deep is dependent upon the correctness of the view that the radial and cutaneous branches of the musculo-cutaneous are distributed solely to skin. Most anatomical textbooks describe the distribution of the radial as "purely" or "solely" cutaneous, and it seems clear that such descriptions induced Head to select the radial and musculo-cutaneous nerves for his experiment and to believe that the residual sensation could be regarded as unaffected subcutaneous sensibility. My own clinical observations have shown that the radial(1), besides supplying skin, is usually distributed to certain articular structures. From a study of fourteen patients in which the musculo-spiral had been severed, it was found that, although in two the recognition of passive movement was perfect in all the joints, in twelve one or more articulations of the thumb or fingers were affected. Such a study really resolved itself into an investigation of the distribution of

sensory branches from the radial and possibly also from the lower external cutaneous branch of the musculo-spiral to the joints, and showed conclusively that it is customary for one or more joints of the outer digits to be supplied by these cutaneous nerves. This was supported by an investigation of the residual sensation in four patients suffering from division of both the median and ulnar nerves and the examination of a fifth patient, who had had the radial and median nerves severed in the forearm. A careful dissection of nerves, which have unfortunately been described as purely cutaneous, shows that a large proportion of fibres terminate in the subcutaneous tissues. Such a gross method of investigation as dissection does not supply any information about the function of these fibres which can be traced to the deeper tissues, but, from the knowledge obtained from the examination of patients suffering from division of the musculo-spiral nerve, it appears certain that a proportion of them are sensory. Consequently we must not assume that any nerve, of sufficient size to justify its selection for experimental work, is purely cutaneous until it has been so proved. The radial is not normally purely cutaneous in distribution and it seems unlikely that any nerve trunk or branch of sufficient size to deserve a specific name, has an exclusively cutaneous distribution. Consequently we cannot separate anatomically the distribution to cutaneous and subcutaneous structures of any sensory nerve sufficiently large to warrant its use as a source of information with regard to sensation, and therefore any subdivision of sensation into cutaneous and deep must be artificial.

In the course of my studies on sensation the extreme difficulty of determining clinically whether the sensory fibres of a nerve are distributed solely to skin or not became manifest, the chief hindrance arising from the fact that we cannot ascertain for certain whether some aspects of sensation are subserved by fibres terminating in skin, or subcutaneous tissues, or both. This difficulty is particularly well illustrated by localisation, which form of sensation can be shown to be subserved by fibres which terminate cutaneously and subcutaneously. When testing localisation by a method which gave measurable results (2), it was found that after division of the median or ulnar the average error for the localisation of a pressure stimulus on the affected side was about 1.6 cm. to 1.8 cm. whereas on the normal hand it was .6 cm. This was found to be irrespective of the level of the division of the nerve and therefore it became important to determine if possible whether this was due simply to a loss of cutaneous sensation or was the result of some disturbance of so-called deep sensibility in addition. According to Head, since this marked difference in the power of localisation on the two sides was found even when the nerve had been divided at the wrist without any division of tendons, it ought to have been due simply to a loss of cutaneous fibres, since he maintains that deep sensibility is subserved by fibres which run mainly with motor nerves and is not affected by division of the median or ulnar at the wrist. Several preparations were applied to the unbroken skin in an endeavour to procure an uncomplicated cutaneous anaesthesia, but these proved unsuccessful until



my colleague, Professor R. B. Wild, suggested a 10 per cent. solution of cocaine hydrochloride in chloroform. By applying this solution to a small area of skin, such as the dorsum of a finger, it was practicable to get a satisfactory anaesthesia to the lightest applications of a fine wisp of cotton wool. By measuring the power of localisation of the same part during anaesthesia and after all its effects had passed off, it was found that it was possible to localise with practically the same degree of accuracy under the two conditions. These experiments showed that when the cutaneous fibres were temporarily eliminated, localisation through fibres terminating subcutaneously was for all practical purposes, as accurate as under normal conditions, and therefore the serious errors in localisation discovered after division of the ulnar or median at the wrist must have been due to interference with the subcutaneous sensory fibres. Therefore we may safely assume that in the case of the ulnar or median this aspect of deep sensibility is only in part at any rate subserved by fibres which run mainly with the motor branches and reach the subcutaneous tissues *via* the tendons. These results were verified in a number of patients suffering from division of the median and ulnar, and were found to hold good also in the one case of division of the radial examined. The latter case is particularly important since it shows that, by means of a measurable test for localisation, we can demonstrate that the radial does sometimes at any rate contain fibres which terminate subcutaneously for this form of sensibility, and lends further proof to the contention that the radial is not a purely cutaneous nerve. Therefore two aspects of deep sensibility (recognition of passive movement and localisation) are affected by division of the radial, median or ulnar nerves at the wrist; and of these two forms localisation only can be subserved, and that partially, by fibres which run with the motor nerves and extend along the long tendons to the hand. It seems possible from my own researches and those of others that discrimination may also be served by both cutaneous and subcutaneous systems, but there are even greater technical difficulties to be surmounted before the question can be decided. At first sight the experiment upon Head's own arm appears to establish discrimination as solely dependent upon a cutaneous supply, but it is built on the *assumption* that the radial and terminal branches of the musculo-cutaneous are purely cutaneous nerves, and, since I have found this is not the case normally, the results cannot be accepted as proof that discrimination is only a cutaneous form of sensation. The extent of the anaesthesia, which it was practicable and safe to procure with the cocaine solution, was too small to be of service for the testing of discrimination.

Sensory fibres concerned with two other aspects of deep sensibility, namely, the appreciation of pressure pain and the mere recognition of the contact of pressure, both of which I have investigated, do seem to run with the motor branches. This is well shown by the fact that these forms of sensation are unaffected by section of the median or ulnar at the wrist, whereas division proximal to the origin of branches for the supply of the long flexors

of the fingers and wrist invariably causes an area of complete loss of all forms of sensation.

It is quite clear that the sensory innervation of the deep tissues of the hand and digits is anatomically complex, and consequently it is exceedingly difficult to elucidate the problems of sensation in this region. After it has been realised that the various aspects of sensation now grouped under the term deep sensibility may be dissociated, it becomes possible to unravel the anatomical problem.

The interphalangeal and metacarpo-phalangeal joints receive their sensory supply from the digital branches of the median, ulnar and radial nerves. The localisation of a pressure stimulus is mitigated partly by branches which arise from these three nerves in the palm and on the dorsum of the hand and partly by branches which arise from the main trunks in the forearm, along with the efferent fibres, and so reach the hand by extending along the tendons. As far as it is possible to ascertain by clinical tests, pressure pain and the mere recognition of the contact of pressure are mainly subserved by fibres which run with the motor branches.

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# A STUDY OF THE CENTRAL TENDON OF THE DIAPHRAGM

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WHAT Haller designates as “nobilissimus post cor musculus diaphragma” has for many centuries been an object of curious enquiry to human anatomists and physiologists, enquiry at times of so highly speculative a nature as, for example, an attempt to recognise in the diaphragm the seat of the emotions—a statement repeated in a French text-book so recently as just one hundred years ago. Such romancing apart, the diaphragm is certainly in many respects unique among the muscles of the body, and no little part of the interest aroused by it has centred in the nacreous trefoil leaf which we know as its Central Tendon. This piece of tendinous tapestry woven of a complex arrangement of aponeurotic fibres, while undoubtedly showing individual variations in the finer detail of the pattern, yet exhibits a very remarkable uniformity of design in different specimens, and in the first place it is here proposed to present what would appear to be the essential elements in this design.

The material on which the present study is based comprises twelve adult diaphragms taken from anatomy subjects after the adjoining viscera had been removed in the ordinary course of dissection, but with the covering fasciae undisturbed; nine diaphragms removed during post-mortem examinations of still-born full-time foetuses; seven foetuses dissected entire, aged from  $2\frac{1}{2}$  months to full-time; and the diaphragms in a young chimpanzee, a Capuchin monkey and a marmoset. For most of the foetal material I am indebted to Dr Cruickshank, Pathologist to the Glasgow Royal Maternity Hospital, and for the comparative material to Sir Arthur Keith, Curator of the Royal College of Surgeons' Museum.

The results obtained in this investigation differ considerably from the published accounts which I have consulted, but the presentment here given would appear to be supported by confirmatory developmental and comparative evidence. Of existing descriptions obtained, undoubtedly the best is that of Bourguery; the better-known account by Poirier would seem to be founded, to a considerable extent, on the earlier work. According to Bourguery, the main elements in the central tendon are two “bandelettes” surrounding the opening for the inferior vena cava. One of these, the posterior semicircular band, passes from the posterior extremity of the right lobe along the whole length of its abdominal surface, sweeps round the vena caval foramen and in front of the oesophageal orifice into the left lobe, at the posterior extremity of which



it ends; horse-shoe shaped, it unites the posterior lobes and forms a protective arch in front of the three great orifices. The other, the antero-posterior oblique band, passes from the right posterior extremity of the central tendon to its left anterior edge; at first on the upper surface above the former band in the right lobe, it forms the internal border of the vena caval opening, separating it from the oesophageal, embraces by two sheets the transverse arch of the first band, and expands into a triangle in the anterior lobe, to the extremity and either side of which it is finally attached.

Poirier, in addition to "fundamental fibres" running obliquely in the lateral lobes and antero-posteriorly in the anterior lobe, describes a "superior bandelette" on the convexity of the tendon, and an "inferior bandelette" on its concavity, corresponding respectively to the oblique antero-posterior and posterior semicircular bandelettes of Bourguery. Poirier's dictum that the central tendon is "the intermediate tendon of a series of digastric muscles" must only be understood in a general sense and cannot be applied to every individual fibre of the tendon.

Dally, in a monograph on the anatomy and physiology of the diaphragm, describes two interlocking U-shaped bands enclosing the vena caval opening between them, the anterior attached by fan-wise expansions to either side of the anterior lobe, its narrow middle portion bounding the vena caval foramen posteriorly, the posterior arising similarly from the extremities of the posterior lobes, with a narrow central portion passing in front of the venous opening.

In all these descriptions, the central tendon is regarded as being founded on two bands, variously described, but always so arranged as to delimit by their intertwining the ellipsoidal foramen for the inferior vena cava. Now this great vein is an asymmetrical structure, derived from the right-hand elements of a series of bi-lateral vessels, and theoretically it would seem strange that a complete transverse body septum such as the diaphragm should be architecturally arranged round a structure developmentally one-sided. In actual fact, the central tendon does exhibit a remarkable symmetry of construction, in many instances even to the extent of reproducing on the left side a miniature replica of the inferior vena caval foramen.

#### STRUCTURE OF CENTRAL TENDON

The general shape of the central tendon is familiar, consisting of a central intermediate area from which three lobes radiate. Of these, one (anterior lobe) is directed forwards towards the xiphoid process and resembles in form an equilateral triangle, joining the central zone along its base, with the sides slightly curved and the apex blunted. The other two lobes (right and left) are rather tongue-shaped, passing obliquely outwards and backwards on either side, the long axis of each curved with a medial concavity, and the left distinctly narrower than the right. Everywhere surrounded by muscular fibres attached to its periphery, the aponeurosis contains within it the opening for the inferior vena cava, lying in the inner half of the line of junction between

right lobe and central zone. Both surfaces are clothed with a distinct fascial layer—below, this is finer and strips off easily; above, it is denser, more adherent, and firmly attached to the pericardium, which is not structurally attached to the central tendon itself except at the very apex of the anterior lobe. Constructed of a multitude of tendinous fibres running singly, or applied to each other in sheets or flat bundles of varying width, the pattern of the interwoven membrane is simpler and relatively homogeneous in each lobe, but in the intermediate area exhibits a more organised system of primary bands binding together the more peripheral parts. The arrangement shows more clearly on the under surface, where the tendon-margin is also sharply defined. Above, on the other hand, the margin is blurred posteriorly because of

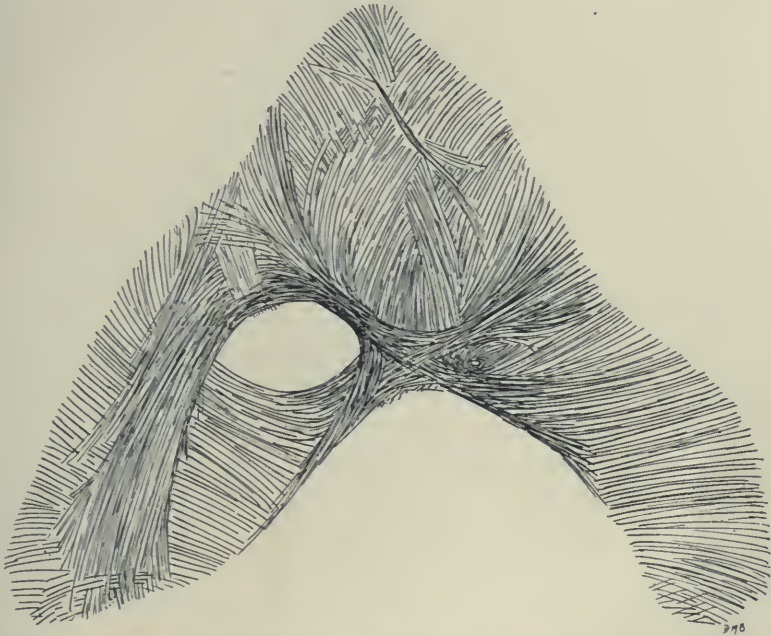


Fig. 1. Arrangement of fibres in central tendon, as seen on the under surface.

a superficial stratum of fine but tough fibres, extending over the muscle fibres, and gradually thinning out as it blends with the covering fascia (figs. 1 and 2).

The simpler arrangements in the lobes may first be described. In the anterior are closely woven fibres passing from the lateral borders and apex, running backwards and inwards in gentle curves, convex forwards, and decussating towards the middle (axial) line of the lobe. Towards the base the fibres run more transversely and towards the apex occasional scattered transverse fibres also occur. The right and left lobes have a common feature, in that they are mainly formed of a sheet of fibres passing transversely to the long axis of the lobe, and running into obvious continuity with muscle fibres on either side; decussation in the axial line of the lobe, if any, is confined to

the tip posteriorly. This (transverse layer) appears clearly on the under aspect, but above it is strengthened and concealed by the stratum of fine fibres previously mentioned. These run longitudinally, but curve in towards the centre of the lobe posteriorly, thus forming a felted decussation. This layer (superior longitudinal), particularly the posterior decussating portion, extends over the muscular part of the diaphragm as a meshwork of fibres which becomes finer and more open towards the periphery. Anteriorly, the longitudinal fibres diverge towards the margins at the "neck" of each lobe, thus exposing on the upper surface the anterior part of the transverse layer; the outwardly-diverging half on each side joins the muscle fibres at the lateral margin where anterior

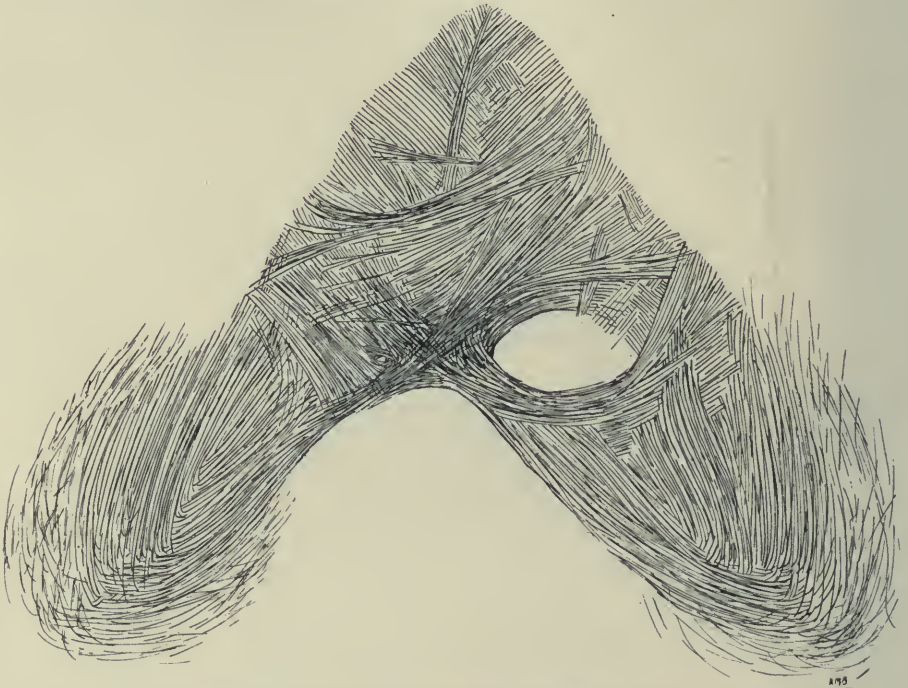


Fig. 2. Arrangement of fibres in central tendon, as seen on the upper surface.

and posterior lobes join. The right lobe shows, in addition, an incomplete third layer in the form of a longitudinal band on the inferior surface (inferior longitudinal layer). Spreading out posteriorly where it arises from the tip of the lobe, its fibres are massed together further forwards as a ribbon-like band sweeping round the outer side of the vena caval opening, antero-lateral to which the outer fibres of the stream join the muscle fibres on the margin of the tendon. It conceals the transverse layer in the middle line of the right lobe and is separated from it just lateral to the venous opening, by the right inferior phrenic vessels passing outwards between the two strata across the neck of the lobe.

Turning now to the central zone, this is found to be occupied by four well-



marked diagonal bands radiating outwards from a central point of decussation like the bars of a St Andrew's cross. This central point appears as a thick node of compressed tendinous strands situated in front of the oesophageal aperture and to the left of the vena caval opening; as the four bands diverge from it towards the various lobes, each expands in fan-wise manner. Regarding them as converging on the central node, each band sends fibres mainly diagonally across the decussation into the opposite band, but also to a lesser extent into each of the adjacent pair. From their relative positions, the bands may be referred to for convenience as right anterior, left anterior, right posterior and left posterior. Each one of the two posterior bands passes backwards and outwards along the inner margin of the corresponding posterior lobe; some fibres then curve outwards across the neck of the lobe and so fall into line with the fibres of the transverse layer, while others pass over or between the transverse fibres and on the upper surface of the tendon run into continuity with the inner half of the superior longitudinal layer. The two anterior bands diverge widely, to become continuous with the more lateral fibres of the anterior lobe and with the muscle fibres on its margin posteriorly and as far backwards as the anterior part of the posterior lobe. Further, each one sends fibres curving backwards into the centre of the corresponding posterior lobe. On the left side this is usually but slightly seen; on the right side, however, a well marked stream of fibres passes backwards round the antero-lateral margin of the caval opening to become continuous with the inner portion of the inferior longitudinal layer. As for the rounded angular intervals between the bands, the anterior is occupied by the more central fibres of the anterior lobe running backwards into the thickness of the central node; the posterior by the muscular fibres of the crura passing up from either side of the oesophageal opening to the posterior part of the central node, which they may slightly overgrow. The right lateral angle forms the foramen for the inferior vena cava, closed laterally by the overlapping of the right anterior and posterior bands (anterior below). The vessel wall is unattached by tendinous fibres to the rounded inner border of the foramen, which is thickened by a characteristic twisted bevelling. In front and behind, a few fine fibres from the margin may decussate on to the coats of the vein, but laterally a well-marked accession of fibres runs from the vessel outwards to the edge of the tendon, strengthening and somewhat obscuring the overlapping already mentioned. Between the left pair of bands is a thinner and therefore slightly depressed area floored by a single layer of fibres, which are continuous with or derived from the adjacent borders of the radiating bands. The floor thus formed by the interweaving of these fibres often exhibits a small perforation transmitting a minute vein.

An examination of foetal diaphragms serves to confirm the arrangements just described. Both in shape and relative size, the central tendon appears to conform to adult proportions. In the youngest foetus dissected (5.5 cm.) the shape is much as in the adult, and the characteristic difference between the two posterior lobes is already distinct. It was noted in this case, too, that the

area of the posterior lobes—as seen from above with the diaphragm in position over the liver—corresponded closely with the portion in contact with the upper surface of the liver, which is moulded on to the vertebral column as a deeply notched crescent with rounded extremities. The concavity of the crescent corresponds exactly to the concave posterior border of the central tendon. In the foetus, the pericardium is readily stripped off the upper surface of the diaphragm, except at the very tip of the anterior lobe, and immediately around the inferior vena cava.

The arrangement of the tendinous strands in the older foetal specimens is the same as in the adult, but the pattern shows with more diagrammatic clearness because of the fewer number of fibres, and the absence of the finer complexities seen in the tougher adult structure. At about six months, only the main fibre-systems are well developed, and a definite tendinous arrangement throughout the whole central tendon is probably not to be seen much earlier than  $4\frac{1}{2}$  months. In the earlier specimens, the four central bands are only to be seen as radiating thickenings when the diaphragm is held up against the light, but under a low power of the microscope the typical arrangement of the individual fibres in the bands and the central decussation is clearly to be made out. The more peripheral parts in the youngest diaphragms examined are formed simply of fibrous tissue in which definite tendinous lines are not yet laid down, but even here the central cruciate arrangement is distinct.

The diaphragm of a 6 months old chimpanzee showed a central tendon fully as tough and as thick as in the adult human, although much smaller, and having a very similar arrangement of strands, including the central decussation. In a Capuchin monkey and still more so in a marmoset, the delicate central tendon (distinctly smaller in comparison with the muscular portion than in man) appeared as an almost transparent membrane save for the bars of the central cross which could be clearly seen against the light. With a low-power objective, however, the arrangement of the delicate tendinous fibres could easily be followed out, and showed all the essential elements of the human pattern. In particular, the optic chiasma-like arrangement of the strands in the central decussation was definitely observed in each case. The whole appearance of the central tendon closely resembled that seen in the human foetus at 3–4 months. In all three monkeys, the vena caval opening lay in the right lateral angle of the cross, and the left angle showed a weaker area with, in the Capuchian monkey, a tiny perforation bounded by backward-turning fibres of the left anterior band. An area similarly bounded, but occupied by a diaphanous membrane in which tendinous fibres were absent, was present in the marmoset.

The inferior vena cava, then, is not the central pillar round which the main bands in the tendon turn, but is merely included in one lateral angle of the cruciform ligament which is in turn the mainstay of the central tendon. Further, the foramen for the inferior vena cava is to be regarded as the functionally enlarged right-hand member of a pair of venous foramina of which the left also, as a rule, still exists, but is very much smaller in size. The latter statement will now be considered in more detail.



## LEFT VENOUS FORAMEN

In dissecting the adult central tendon, it is not uncommon to find minute veins passing through the tendon by apertures which appear as slit-like intervals between parallel fibres. These are seen chiefly in the posterior part of the anterior lobe, in the angle between the right and left anterior bands. It is to such that Cloquet probably refers when he says: "Au devant de (foramen venae cavae) il n'est pas rare d'en trouver deux ou trois autres, qui traversent obliquement l'épaisseur de l'aponeurose et livrent passage aux veines diaphragmatiques inférieures et sus-hépatiques." Morgagni, in five of his post-mortem records, notes the occurrence of multiple venous foramina in the central tendon, two or three in place of the usual one, but does not always give details of position. One case is evidently that of a subdivision of the usual

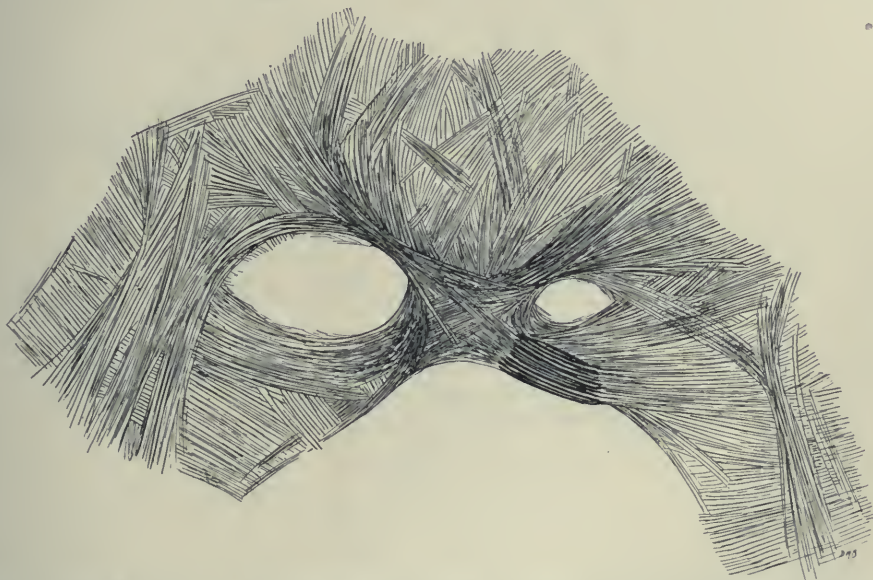


Fig. 3. Central portion of central tendon exhibiting a large left venous foramen, as seen from below. (An abnormal muscular slip partly obscures the left posterior band in this specimen.)

caval opening—"tenuissimo quidem interstitio, sed evidentissima divisa." In another, an additional opening immediately in front of the caval foramen apparently transmitted one of the usual hepatic veins which then joined the inferior vena cava above the diaphragm instead of below it, as normally happens.

The foramen to which attention is here directed, however, is almost constant in occurrence, although it varies in size. It is not an artefact or mere slit between parallel fibres, but occurs in a definite position and is definitely marked off in the weaving of the tendon. Such a foramen was seen in ten of the twelve adult diaphragms examined; the size of the largest was  $15 \times 7$  mm., admitting the tip of the little finger (fig. 3); two measured  $4 \times 3$  mm. and the



remainder were more minute. In each case the perforation lay exactly in the angle between the left pair of bands and was circumscribed laterally by a few fibres of the left anterior band curving back into the left lobe. In the better-marked instances, the inner border of the foramen showed the twisting characteristic of the caval opening, with fibres of the left anterior and left posterior bands curving into continuity with each other. At the outer border, the backward-turning fibres of the left anterior band passed on the ventral face of the left posterior fibres, approximating in one case to the formation of an inferior longitudinal layer of the left side. In the full-time foetus this foramen is also usually to be seen, but in the younger diaphragms it is at times

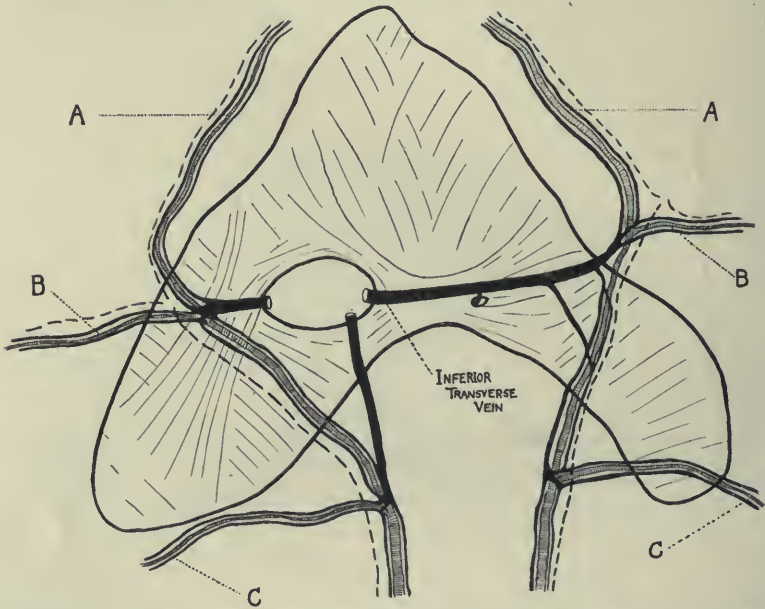


Fig. 4. Diagram to show general arrangement of the main blood-vessels on under surface of central tendon. A=anterior; B=middle; C=posterior divisions of each inferior phrenic artery. (Arteries represented by barred, veins by solid, and nerves by interrupted lines.) N.B. The right inferior longitudinal band is represented as transparent, as the vessels of the right side pass *above* it.

rather difficult to establish beyond doubt either its presence or absence on account of the smallness and delicacy of the parts. In all such cases, however, the left angle of the cross shows a markedly weak area where the tendinous fibres seem to be replaced by a structureless fascia. Sometimes a distinct perforating vein attached by the fascia to the margins of what is at any rate a deficiency in the tendinous structure can be seen to pass through this area. Whenever present, in adult or foetus, this left foramen is traversed by a small vein, to understand the connections of which a somewhat full consideration of the blood vessels of the diaphragm is necessary (fig. 4).

## DIAPHRAGMATIC BLOOD VESSELS

On either side, the inferior phrenic artery is to be seen ascending upon the abdominal aspect of the corresponding crus of the diaphragm and then turning obliquely outwards across the posterior lobe of the central tendon at about the junction of its anterior and middle thirds; at this point the vessel on the right side passes deeply to the inferior longitudinal band. The artery is distributed by three main divisions. The first of these (posterior branch) usually arises before the vessel crosses the central tendon and passes backwards and outwards beyond the tip of the posterior lobe. After crossing the tendon, the main artery bifurcates into the middle branch, passing outwards amidst the muscle fibres, and the anterior branch running forward parallel with the lateral border of the anterior lobe of the central tendon. The terminal division on the right side usually occurs just before the vessel escapes from under cover of the inferior longitudinal layer. The phrenic nerve, dividing into terminal branches, pierces the diaphragm close to this final bifurcation of the artery—distinctly in the fleshy part on the left side, sometimes through the outer angle of the caval foramen on the right side, but more usually the right nerve goes through the tendon lateral to this, or even on the musculo-tendinous junction line. One main branch then usually accompanies the anterior branch of the artery, another accompanies the middle arterial branch, and a third, passing backwards along the stem of the inferior phrenic, supplies the crus on its abdominal aspect. Other finer terminal twigs of the nerve run more irregularly.

The three divisions of the inferior phrenic artery are accompanied by *venae comites*. Those with the anterior and middle divisions unite near the outer margin of the central tendon to form a single channel. This runs transversely into the inferior vena cava—on the right side after a very short course deep to the inferior longitudinal band, while on the left the corresponding vessel forms a large vein (inferior transverse vein) running over the central node of the tendon, and is joined by a twig from the *venae comites* of the posterior arterial branch. Corresponding to this last vessel a distinct vein on the right side ascends on the right crus to join the posterior aspect of the vena cava just before it pierces the diaphragm.

Where the vessels cross the musculo-tendinous junction line, they are sometimes bound down to the abdominal surface of the diaphragm by slender accessory tendinous strands, and the inferior fascia of the diaphragm also serves to hold the vessels in contact with the central tendon.

The large inferior transverse vein is a prominent and almost invariably constant feature on the under aspect of the intermediate zone of the tendon. As it crosses the left foramen, if such be present, it gives off a small perforating branch which passes through the foramen, and in favourable cases is then seen to join a superior transverse vein (much smaller than the inferior and with less definite connections), running from left to right on the upper surface of the

diaphragm and ultimately ending in the supra-diaphragmatic inferior vena cava. Where the perforating vein joins the superior transverse vein, it is usually joined by a distinct tributary derived from the anterior wall of the oesophagus. In one instance the perforating vein was accompanied by a long, fine branch from the left inferior phrenic artery—in another, by a similar branch from the artery of the right side. This venous circle formed by the two transverse veins both joining the inferior vena cava on the right and being themselves joined by the perforating vein on the left, was traced in four out of ten adult diaphragms in which it was sought for, and in four out of nine full-time foetal specimens. The upper part of the loop is under cover of the pericardium, as the left venous foramen is usually situated just within the margin of the pericardial area of the central tendon.

#### PERFORATING VEIN

The position of the perforating vein and the similarity in construction of its foramen to that of the inferior vena caval opening suggests that this little vein may be a vestigial left-sided homologue of the inferior vena cava at this level—to be compared with the somewhat analogous correspondence between the oblique vein of Marshall and the superior vena cava. The inferior vena cava as it pierces the diaphragm represents the enlarged upper part of the right vitelline vein, re-constituted, after being broken up in the liver, to form the right hepatic vein. The left vitelline vein in the embryo on its way to the left horn of the sinus venosus is similarly interrupted in the liver, but its upper portion is usually believed to disappear completely at a very early stage, the *venae revehentes* which would otherwise go to form a left hepatic vein joining the vein of the right side. The occurrence of the perforating vein suggests that the supra-hepatic portion of the left vitelline vein (*i.e.* left hepatic vein) is not obliterated so completely or so early—at any rate, not before the primary construction of the central tendon of the diaphragm is laid down.

The presence of further persisting portions in the track of the original left vitelline stem above or below the diaphragm could not, of course, be traced in the adult or still-born foetal specimens, as the adjacent viscera had been previously removed. A search in the seven foetuses dissected entire, however, revealed in two cases a vein leaving the upper surface of the left lobe of the liver independently, between the layers of the left triangular ligament, having arisen within the liver from a vessel appearing to correspond to the *vena hepatica sinistra superior* of Mall's nomenclature. In one case (8 cm.) this vessel turned medially to join the inferior vena cava, first communicating with the inferior transverse vein. In another (13.5 cm.) this left hepatic vein joined the inferior transverse vein at right angles just where a distinct perforating vein was given off; a similar arrangement was found on examining a 30 mm. embryo (longitudinal sections) in the Glasgow University collection, although the delicacy of the vessel walls at this stage, and the lack



of injection, rendered accurate tracing of the fine veins involved a somewhat difficult matter. The venous circle already described was identified, and the inferior transverse vein, lateral to the point of origin of the perforating vein, appeared to be joined by two very fine veins which had arisen within the liver from the vena sinistra superior. This connection seemed to be in process of obliteration—in the other two it had so far persisted as to be readily traced by ordinary naked-eye dissection (fig. 5).

In such cases there would appear to be vestigial traces of the upper part of the left vitelline vein issuing from the left lobe of the liver and passing upwards through the diaphragm towards the heart. As for the next and final stage in the course of the vein, from diaphragm to left horn of sinus venosus, no trace was found, unless it be in the more or less constant tributary of the superior transverse vein descending in front of the oesophagus and draining

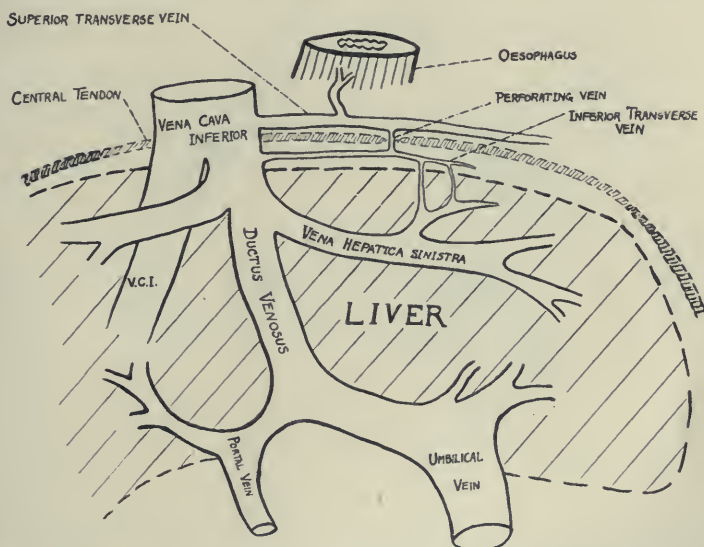


Fig. 5. Diagrammatic reconstruction of conditions found in 30 mm. embryo.

the plexus of veins on the oesophageal wall. This absence of any trace of such a vessel is not surprising when one considers how early and how completely the original relative positions are modified, whereby the left horn of the sinus venosus is removed from all contact with the developing diaphragm and carried upwards as a result of the bending and twisting of the primitive heart tube. It is, however, suggested that vestiges of the supra-hepatic portion of the left vitelline vein are to be recognised in this occasionally occurring vein issuing independently from the left lobe of the liver, and in the much more commonly occurring perforating vein of the diaphragm.

## ACCESSORY MUSCULAR SLIPS IN CENTRAL TENDON

In the series of diaphragms examined in the course of this study, abnormal muscular slips were found to occur so frequently in the central tendon as to merit a final note on this point. No examples were found of slips attached to the liver or peritoneum, as have been occasionally noted as diaphragmatic abnormalities; the accessory muscles met with were entirely diaphragmatic in their attachments, lying either on the abdominal aspect of the central tendon or in its thickness, but never on the superficial aspect of its upper surface. They occurred in six out of sixteen foetal diaphragms—in three of these two slips were present, while in another there were no less than four. Five out of twelve adult specimens showed abnormal slips, in two cases out

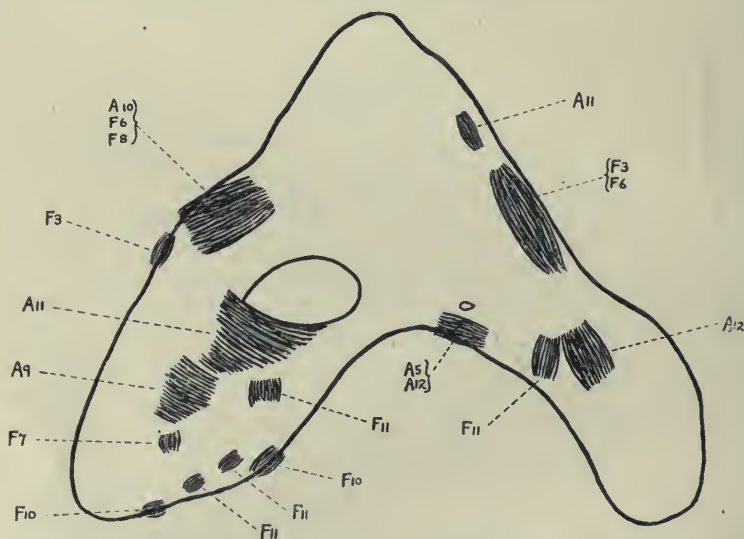


Fig. 6. Diagram to show approximate position of abnormal muscular slips in the series of diaphragms examined. The figures refer to the serial numbers of the specimens in which the particular slips occurred. *A*=adult; *F*=foetal.

of the five two slips being present. The different positions occupied by these slips is indicated in the accompanying diagram (fig. 6).

Most commonly they occurred as flattened fleshy bellies with narrowed extremities attached by tendinous fibres to the central tendon or the covering fascia; in two adult cases they took the form of muscular replacement of portions of the transverse layer of the right lobe—in one of these the intermediate portions of the transverse fibres were replaced by muscle for a distance of 3–4 cms. behind the posterior border of the caval opening. In the Capuchin monkey and comparable with the last case the vena caval foramen was bounded posteriorly by a pointed muscular slip continued inwards from the muscular portion of the diaphragm almost to the inner angle of the foramen. Such occurrences are reminders of what is seen in some other mammals where the

“central tendon” is almost wholly fleshy, as in the pole-cat (Le Double), or entirely so, as in the porpoise (Poirier, Le Double). Le Double also mentions the curious fact that the central tendon in the dromedary encloses a bone, and Morgagni records finding an osseous patch in a human diaphragm.

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[The illustrations in this article have been published  
with the aid of a grant from the Carnegie Trust.]



## A CASE OF CONGENITAL MALFORMATIONS OF THE INTESTINAL CANAL

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CONGENITAL malformations of the intestine giving rise to congenital intestinal obstruction are well known, but this case presents some features which are far from common.

The history of the case was as follows:

The child, a male, was admitted to King's College Hospital two hours after birth with complete absence of the anus. It was the first child and was premature by two weeks. There was no sign of an anus or dimple to mark its position. I made an incision in the perinaeum, but no sign of rectum was found although the wound was explored for a depth of one and a quarter inches from the surface. The wound was stitched up, a laparotomy performed, and a portion of the descending colon was quickly brought to the surface; a small piece of tubing was inserted into the colon and the wound closed. No meconium was passed by the colostomy opening and the child died three days after admission.

On making a careful dissection of the abdomen it was found that the descending colon opened into the prostatic urethra just to the left of the mid-line. A Meckel's diverticulum was present. The stomach was somewhat distended and the duodenum was greatly distended and was larger than the stomach. At the duodeno-jejunal flexure there was a complete septum across the gut through which the smallest probe could not be passed. The rest of the intestine was normal (fig. 1). There were two accessory spleens.

The existence of three or more congenital defects in one subject suggests the question as to their causation. Are all three defects due to a common cause or have they occurred independently? The frequency of multiple congenital abnormalities in single individuals appears to indicate that there is a common cause. Previous cases of congenital abnormalities which have come under my notice, lead me to believe that the common cause is defective nutrition of the embryo in the early stages of growth, leading to arrest of the normal process of development.

The peculiar features of this particular case may all be explained as persistences of early conditions.

(1) The persistence at the site of the septum, of the epithelium, which completely fills the lumen of the gut in the duodeno-jejunal region in embryos of about 6 mm. in length.

(2) Persistence of the intestinal end of the vitello-intestinal duct.

(3) Persistence of the cloacal condition of the embryo which has given rise to a recto-urethral fistula.

The cloacal stage in development is seen to be present in a human embryo

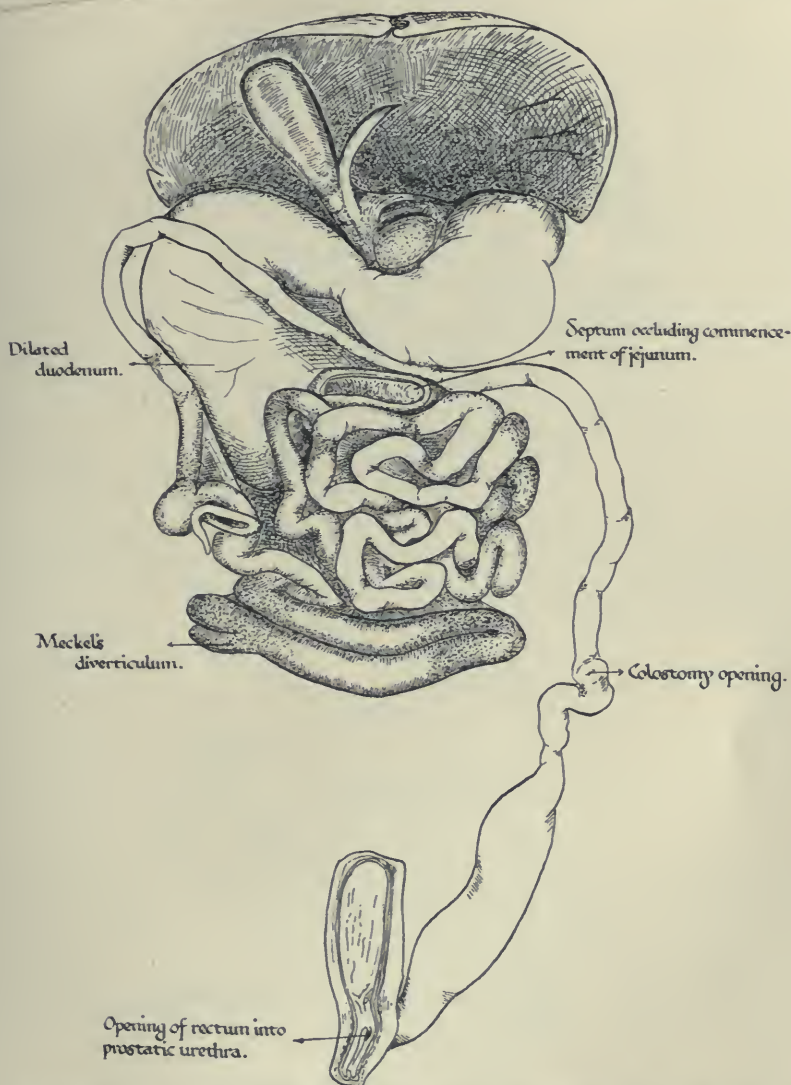


Fig. 1. Front view of the abdominal and pelvic viscera which have been removed from the body. The greatly distended duodenum, which is crossed by the transverse colon, has been opened near its termination in order to show the occluding septum between it and the jejunum. In the lower part of the drawing are seen the colostomy opening, and the opening of the rectum into the prostatic part of the urethra.

of 12 mm. in length and about five weeks old (fig. 2). In a medial sagittal section of a rabbit embryo 15 days old and measuring 13 mm. in length, the

urorectal septum is seen to be in contact with the cloacal membrane thus shutting off the rectum from the pars phallica of the urogenital sinus (fig. 3). A similar stage has been modelled by Professor Hochstetter, in a human embryo



Fig. 2. Sagittal section through the cloacal region of a human embryo, of 12 mm. greatest length, showing the urorectal septum, situated between the rectal and ventral parts of the cloaca. The union of the urorectal septum with the cloacal plate has not yet occurred. The post-anal gut has completely disappeared.

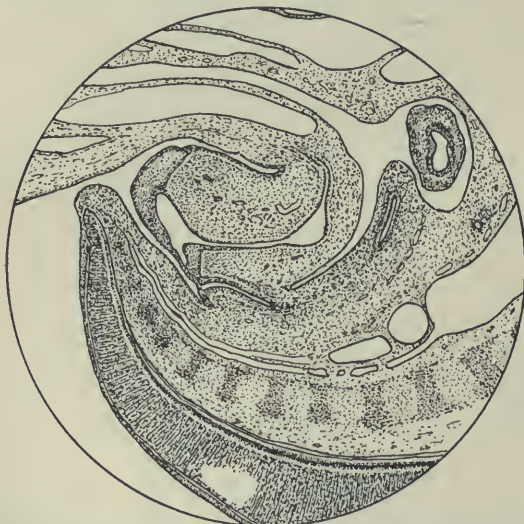


Fig. 3. Sagittal section through the cloacal region of a rabbit embryo, of 15 days, and 13 mm. greatest length, showing the fusion of the urorectal septum with the cloacal plate. No vestiges of the post-anal gut are present.

of 11 mm. At this stage, the lower ends of the Wolffian duct and ureter open by a common orifice in the vesico-urethral part of the ventral cloaca which is



separated from the cloacal membrane by the whole length of the urogenital sinus. In the early stages of development represented by embryos of 4 mm. in length the lower opening of the Wolffian duct opens close to the cloacal membrane and below the level of the intraclacal anus.

It is probable therefore that the defect in the specimen I have described, must have occurred at an early stage when the opening of the Wolffian duct was near the level of the lower margin of the urorectal septum and consists of a failure of the union of the urorectal septum with the cloacal membrane.

The frequent termination of the rectum in the prostatic urethra has been explained by Professor Wood-Jones on the supposition that the "tail-gut," which he postulates grows downwards in the human embryo from the termination of the hind-gut in the cloaca to the proctodaeum, has failed to develop, and that consequently the hind-gut retains its original opening into the cloaca, just below the recto-vesical pouch of the peritoneum. This opening he defines as the intraclacal anus. That part of the intestinal tract which lies below the level of the rectovesical pouch in the human subject ends at the posterior extremity of the ectodermal cloaca, on the "anal slope" of the genital eminence, and does not accompany the notochord into the tail as in the marsupialia, in which there is a long post-anal gut which afterwards becomes cut off from the cloaca, and disappears. Such a post-anal or caudal-gut may be developed as an abnormal condition in the human subject, and may give rise to congenital cysts in the region of the coccyx, or an intestinal fistula in connection with a spinal meningocele and is probably due to persistence of the neurenteric canal. A prolongation of the gut has been described into the ventral part of the penis, and opening under cover of the prepuce beneath the glans. In this deformity the penis is traversed by two channels: (1) the urethra, formed from the "pars phallica" of the urogenital sinus, and (2) the intestinal part most probably formed as a prolongation of the cavity of the hind-gut into the ventral cloacal septum or urethral plate.

In a normal human embryo of 20 mm. greatest length, obtained by operation and in excellent condition, the rectum was found to have already opened on the surface at the posterior end of the ectodermal cloaca. In this specimen no sharp line of demarcation between the epithelium of the anal region and that of the intestine can be detected, and although there is a diminution of calibre below the rectovesical pouch, and at the level of the entrance of the vasa deferentia into the urethra, there is no sharp transition between a segment of the channel which might be described as "caudal-gut" and an upper segment the "hind-gut."

It would appear therefore from the study of this and other specimens of human embryos that the exact position of the junction of the proctodaeum with the rectum, whether at the "white-line" of Hilton or at the edges of the anal valves, or the position of the junction of the "caudal-gut" with the "hind-gut" (or dorsal part of the cloaca) cannot be localised with certainty in the adult.

The question as to whether the rectum is divided by a recto-urethral septum into a ventral (vesico-urethral) and a dorsal (rectal) part, or not, has been definitely settled in the affirmative by the excellent models of the cloacal region made by Keibel, Felix and others in the human subject, and by Dr G. Buchanan and Dr E. A. Fraser in the marsupialia. Cases such as the double channel penis mentioned above however appear to support Professor Wood-Jones' contention with respect to the prolongation of the lumen of the gut as an independent channel which is developed as an outgrowth from the cloaca towards the surface. The channel however is apparently formed in the epithelium of the ventral cloacal septum, and is not a diverticulum of the cloacal wall, similar to the "tail-gut" of the marsupialia.

My best thanks are due to Dr R. J. Gladstone, of King's College, London, for so kindly allowing me to have the use of his embryological material, from which the stages represented have been chosen.

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# THE PRIMORDIAL CRANIUM OF *XERUS* (SPINY SQUIRREL) AT THE 17 AND 19 MILLIMETRES STAGES

BY PROFESSOR FAWCETT

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Two embryos were cut, one of the 17 mm. stage and one of the 19 mm. stage. Only one (of 17 mm. stage) was modelled. The results are of considerable interest. The model shows, amongst other things, four hypoglossal canals, each of which is occupied by a root of the hypoglossal nerve. So far as I know, this is the only mammal in which such a condition has been recorded. The superior semicircular canal is almost isolated by a very deep "fossa subarcuata interna." The lamina parietalis is remarkable in dividing anteriorly into two processes, one inferior and the other superior. The inferior one ends freely, whereas the superior is connected with the ala orbitalis by the orbito parietal commissure. The central stem is interesting because it preserves at this stage the three primitive parts (Pl. I) which seem to be typical of the base of the cranium in mammals at least. The hindmost part is entirely hypochordal. The ala temporalis is perforated by an ali-sphenoidal canal. The stapedia artery perforates the stapes and is of large size. There is a common paraseptal cartilage (fig. 1) which anteriorly is joined with the paries nasi by a lamina transversalis anterior, under which runs the naso-lacrimal duct. There is a lamina transversalis posterior.

## GENERAL DESCRIPTION OF THE PRIMORDIAL CRANIUM

### I. *Central stem* (Pls. I, II)

This is divisible into

- (1) A pars chordalis.
- (2) A lamina polaris (Noordenbos<sup>1</sup>) or lamina hypophyseos (Terry) or pars trabecularis (Fawcett).
- (3) A pars interorbito-nasalis.

The pars chordalis is entirely hypochordal from end to end. It commences behind as the anterior boundary of the foramen magnum. It terminates in front at a foramen which is the basicranial fenestra, dividing on each side of this fenestra to unite with the pars polaris. Postero-laterally the pars chordalis is continuous with the ex-occipital cartilage, but the line of continuity is interrupted by the four hypoglossal canals, alluded to previously. Intermedio-laterally the pars chordalis is free and forms the medial boundary of the jugular foramen. Antero-laterally, it is separated by a basicochlear fissure from

<sup>1</sup> Noordenbos. Petrus Camper. 3rd Deel, 1905.



the pars cochlearis of the auditory capsule. Only at its extreme antero-lateral corner is it actually fused with neighbouring parts of the chondro-cranium, i.e. with the pars polaris and pars cochlearis through the medial carotid commissure.

Its intracranial surface is concave from side to side and from end to end. Extracranially it is slightly convex from side to side, but in its cranial half it is comparatively flat and, owing to its thickness in this region, separated by the very deep basi-cochlear fissure from the cochlear capsule.

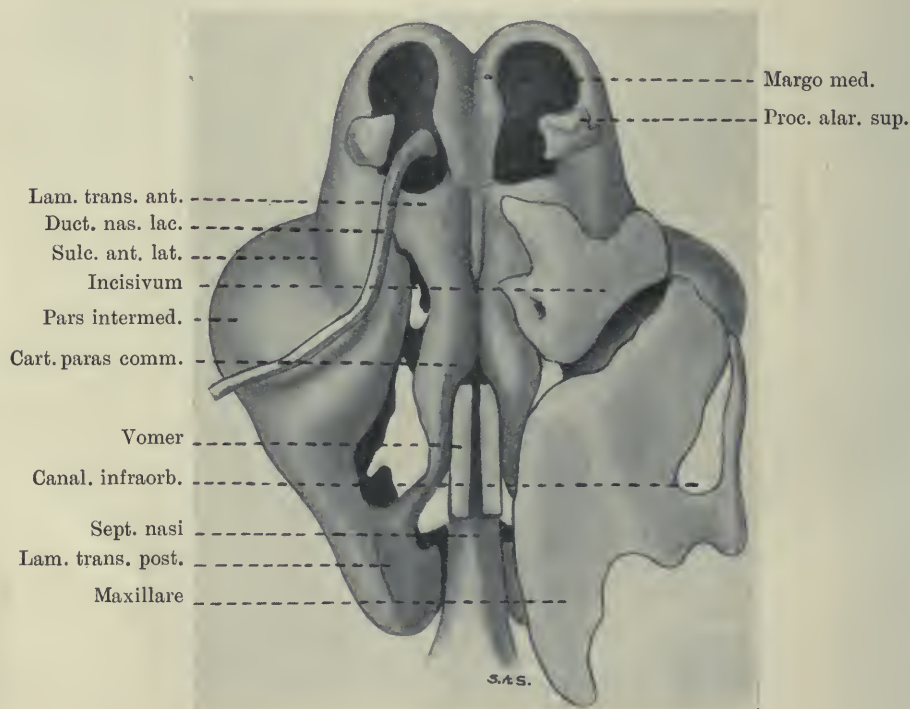


Fig. 1.

## II. *Pars polaris, hypophyseos, trabecularis or pars intermedia.*

This segment of the base has received various names. It is a little doubtful whether any one of them is the most desirable. In a sense, the substitution of the name "pars intermedia" would be preferable, in which case the terms pars anterior and pars posterior would be substituted for those used by the author in previous communications. The difficulties arise when one has to describe the processes which connect this segment of the base with neighbouring parts. In general form, this segment, as seen from above or below, is quadrilateral and is comparatively flat from above or below, i.e. intra-cranially or extra-cranially. Its inclination is almost in the same plane as that of the pars posterior (chordalis). It does, however, actually form an angle with this

part but it is a very obtuse angle, about  $160^{\circ}$ . Its borders are anterior or superior, posterior or inferior and lateral.

The anterior border is overlain by the hinder edge of the lamina hypochiasmatica, from which it is separated by a narrow fissure. Its posterior or inferior border is free about its middle part where it forms the anterior wall of the basicranial fenestra. Lateral to this free part, the posterior border is connected or fused with the pars posterior and with the pars cochlearis, with the latter through the medial carotid commissure. The lateral border from behind forwards consists of three parts, viz. a free part which is the medial wall of the carotid canal; a part which gives off the lateral carotid commissure in common with the processus alaris (the lateral carotid commissure is the alicochlear commissure of authors generally); the most anterior part which is free and forms the medial wall of the superior orbital fissure.

*Pars interorbito nasalis* (Pls. I, II). This commences behind in a flat plate which is inclined at right angles to the pars intermedia, on whose anterior or superior border it rests, separated from it by a narrow fissure. This plate is equal in width to that of the pars intermedia. In thickness, from above downwards, it is about equal to that again of the pars intermedia. Its antero lateral angles receive the post-optic roots of the alae orbitales and they project freely forwards below the optic foramen to form on each side an ala hypochiasmatica from which the rectus system of muscles takes origin. In front of each ala hypochiasmatica (Pls. I, II) is attached one limb of the pre-optic root of the ala orbitalis. This transversely disposed hypochiasmatical segment of the pars interorbito-nasalis is succeeded by a sagittally directed part which for a short distance forms a part of the inner wall of the orbit and is therefore interorbital, but is very soon placed within the nasal capsule of which it constitutes the septal part. This sudden change from a transversely to a sagittally directed cartilage is very striking and is unusual. The arrangement suggests that of the letter T inverted. Once included within the nasal capsule the nasal septum rises rapidly in height, reaching its maximum height at the level of the crista galli. Beyond this the height gradually diminishes chiefly because the upper edge descends. The lower edge remains practically constant. The upper edge in its hinder part is intracranial and it looks almost backwards and to it is attached in its hinder part the anterior limb of the pre-optic root of the ala orbitalis. Its greater part is free and at this stage unconnected with any lamina cribrosa. The extracranial part lies at the bottom of a slight sulcus, the sulcus dorsalis nasi (Pl. I). Anteriorly the septum appears to bifurcate into two curved plates which bound the anterior nares medially and end below in an outwardly curved free process. The inferior margin of the septum nasi is convex from side to side and is placed first between the posterior cupulae of the nasal capsule and later between the two common paraseptal cartilages. Not far from its anterior extremity the septum is continuous with the paries nasi through the lamina transversalis anterior. In front of this, small lateral projections are given off which correspond with the processus laterales ventrales.

*Structures appended to the central stem* (Pls. I, II). These are, from behind forwards,

- (1) Ex-occipital cartilages.
- (2) Auditory capsules.
- (3) Processus alares and alae temporales.
- (4) Alae orbitales.
- (5) Lateral nasal capsules.

*Ex-occipital cartilages.* These are confluent histologically and anatomically with the postero lateral angles of the pars chordalis of the central stem.

Their junction is only indicated by the presence of the four hypoglossal canals, previously mentioned, which range behind one another in a sagittal direction. The two more anterior foramina are small and about equal in size. The two more posterior foramina are large and are also of about the same size. At the lower margin of the root of the ex-occipital cartilage, a condyle is developed. This extends more on to the chordal plate than is usual at such a stage. The ex-occipital cartilage soon passes underneath the corresponding part of the auditory capsule, and on doing so becomes triangular in section. One surface, the dorsal surface, which lies underneath the auditory capsule is formed on what is usually spoken of as the alar lamina. When traced forwards, this alar lamina projects freely as a processus paracondyloideus. The outer edge of the alar lamina is fused with the auditory capsule for a considerable distance, consequently the recessus supra-alaris which separates this alar process from the auditory capsule does not communicate with the exterior. The inferior, extracranial surface is grooved from side to side forming an area paracondyloidea and this groove is limited laterally partly by the processus paracondyloideus and partly by the crista arcuata occipitalis (Pl. II) which is very well developed. There is an internal surface which helps to form the entrance to the foramen magnum from above. Each ex-occipital is continuous at its posterior extremity with the supra-occipital cartilage or tectum posterius.

*Auditory capsule* (Pls. III, IV, I, II). The auditory capsule may be described as consisting of a pars canicularis and a pars cochlearis, and the latter may be further subdivided into cochlear and vestibular segments. The pars canicularis is much of the usual form found in mammals. It presents for inspection medial, lateral and inferior surfaces. The medial surface is deeply indented by the fossa subarcuata interna which is limited above, behind and below by the superior or anterior semicircular canal. Above and in front of the fossa subarcuata there is a slight eminence which is the eminentia ampullaris anterior or superior. From this eminence springs the outer end of the commissure suprafacialis which is of large size. Additionally there is attached to this region the lamina parietalis by means of the parieto-capsular commissure. The medial surface below and anterior to the fossa subarcuata is formed by the crus commune of the anterior and posterior semicircular canals. This crus is grooved on its medial aspect by the ductus endolymphaticus.



The inferior surface is directed towards the lamina alaris of the ex-occipital cartilage. It is grooved from before backwards forming an inferior arcuate fossa, which is bounded on the lateral side by the *prominentia semicircularis posterior*. The cartilage in this region is very imperfectly formed—in fact in the anterior part it is absent altogether. This is a common feature in early chondrocranial development. The external or extracranial surface has a roughly triangular outline. The base of the triangle is placed forwards and shows from above downwards the following parts:

A process, the *tegmen tympani*, which projects forwards over the *Malleus* cartilage. Below the *tegmen tympani* there is a shallow fossa *incudis* and below this a *crista parotica* to which is attached by dense cellular tissue the styloid process. Below the level of the *crista parotica* comes the *processus mastoideus* which is of considerable size and convex in form.

The upper border stretches upwards and downwards to terminate at the cupula. It is formed to a large extent by the anterior or superior semicircular canal and it gives origin in its anterior half or so to the parieto-capsular commissure.

More posteriorly it is free, forming the anterior boundary of a large fissure which is interrupted near its upper end by a very slight attachment of the supra-occipital cartilage to the auditory capsule. The upper segment of the fissure may be called parieto-capsular and the lower occipito-capsular. The cupula is concealed from view externally by the overlap from behind of the supra-occipital cartilage. This overlapping cartilage I have elsewhere termed the operculum of the supra-occipital cartilage. It is not to be confused with the *processus opercularis* of *Talpa*, which is a process directed upwards from the auditory capsule itself.

The inferior border is formed by the posterior semicircular canal. It is fused for a considerable part of its extent superficially with the alar lamina of the ex-occipital cartilage. Behind this fusion it is free where it forms the anterior boundary of the occipito-capsular fissure. The actual lateral surface shows behind the *crista parotica* a swelling which was caused by the lateral semicircular canal—*prominentia semicircularis lateralis*; above and behind which is a *prominentia arcuata*, caused by the projection of the fossa *arcuata interna*.

*Pars cochlearis* (Pls. I, II). This consists of vestibular and cochlear segments. The vestibular segment shows on its medial surface the internal auditory meatus, which is overhung by the suprafacial commissure, a commissure of large size, projecting from the region of the *prominentia ampullaris superior* to the base of the cochlear segment of the *pars cochlearis*. A *crista falciformis* separates the floor of the meatus into upper and lower parts. The upper part which lies above and external to the lower part shows, more medially, the facial canal for the facial nerve, and more laterally the *foramen acousticum superius* for the superior division of the vestibular division of the auditory nerve. The lower part is a large, almost circular orifice which is the

foramen acusticum inferius. It is not completed at present by any cribrous plate, but from its postero-inferior quadrant there runs back a foramen singulare to the ampulla of the posterior semicircular canal.

The inferior surface of the vestibular segment is directed downwards and is for the most part occupied by a somewhat jagged opening which is the common orifice of the foramen perilymphaticum and the foramen cochleae.

The lateral surface shows from above downwards, firstly the sulcus facialis and secondly a very large foramen vestibuli, which is partly occupied by the foot piece of the stapes. The large size of this foramen is no doubt due to the imperfect chondrification in this region. Below the foramen vestibuli, quite a prominent *prominentia cochleae* caused by the first turn of the cochlea, exists.

*Cochlear segment.* The cochlear segment has a medial surface, a superior surface and a surface which may be described as anterior and wholly extracranial. The medial surface consists of two parts; a part which is directed coronally and is almost flat; and a part in front of this which is directed medially and becomes confluent with the dorsal surface of the *pars chordalis* of the central stem.

The superior surface is slightly hollowed and is bounded anteriorly by a ridge which, when traced outwards, projects in that direction for a considerable extent as a slightly hooked process arching over the great superficial petrosal nerve. It does not at this stage enclose this nerve in a foramen. The medial end of the ridge is confluent with the lateral carotid commissure. The *pars cochlearis*, when viewed from above, is seen to be connected with the *pars intermedia* of the central stem by two commissures, namely medial and lateral carotid commissures.

The anterior surface is wholly extracranial and is the largest of the three surfaces of the cochlear segment. It is separated by a very deep sulcus from the *pars chordalis* of the central stem. This may be called the *basi-cochlear sulcus*. At the bottom of this sulcus at the 17 mm. stage, a narrow fissure leading into the cranial cavity is the *basi-cochlear fissure*. The fissure is obliterated at the 19 mm. stage, but the sulcus retains its original depth. The fissure is bounded posteriorly by a commissure, the *chordo-cochlear commissure*. About the centre of the anterior surface, the cochlea forms its cupula and from the region of the foramen vestibuli of the vestibular segment, there runs inwards a *sulcus septi* which corresponds with the septum in the cochlea. The *manubrium mallei* comes almost into contact with the cochlear segment in this groove.

*Processus alaris and ala temporalis* (Pls. I, II). The *processus alaris*, at this stage, has a common origin with the lateral carotid (alicochlear) commissure from the *pars intermedia*. Ultimately it projects laterally beyond that commissure and reaches the *ala temporalis*. Postero-inferiorly it fuses with the *ala temporalis*, but anteriorly and superiorly, it is separated from the *ala* by a V-like fissure, which is occupied by a wedge-shaped mass of dense cellular

tissue. The pterygoid bone, ending below in a cartilaginous hamulus, lies to the medial side of the terminal part of the processus alaris.

*The ala temporalis.* As has been mentioned, the ala temporalis is only partially fused with the processus alaris. The ala is at first directed outwards, it is thick from above downwards and comparatively thin from before backwards. The projecting lower end may be regarded as a pterygoid process. Beyond this, the whole ala is directed upwards and outwards, forming the so-called lamina ascendens. At the junction of the ascending with the horizontal part a large ali-sphenoid canal is found perforating the ala from behind forwards. This canal seemed to be occupied by veins and connective tissue. It did not transmit the internal maxillary artery. The upper aspect of the ala is concave from side to side, and the concavity lodges the maxillary division of the fifth nerve. The ala temporalis very nearly reaches the posterior basal angle of the ala orbitalis. It is separated therefrom by the supra-orbital artery. To the medial side of the ala, at its root, is placed the palate bone.

*Ala orbitalis* (Pls. I, II, III, IV). The ala orbitalis is a large triangular plate, convex from before backwards on its intracranial aspect and correspondingly concave on its orbital surface. Its apical part divides into two branches of which the more posterior is attached to the lateral margin of the lamina hypochiasmatica (trabecularis). This is the taenia metoptica.

The anterior branch, otherwise the taenia preoptica, divides into anterior and posterior rami. The posterior ramus descends with a slightly backward course to reach the antero-lateral angle of the lamina hypochiasmatica. The anterior ramus, much broader than the posterior, fuses with the upper part of the cupula nasi posterior and at the same time with the upper lateral edge of the interorbital septum. Between these two branches and the interorbital septum the foramen prechiasmaticum is situated. This, at the 17 mm. stage, is a long slit. By the 19 mm. stage it has become very considerably reduced in length, owing to the increasing breadth of the two divisions of the pre-optic branch of the ala orbitalis. The posterior basal angle of the ala orbitalis is fused up with the orbito-parietal commissure. The anterior basal angle fuses with the cranial margin of the prominentia frontalis of the nasal capsule. Between the anterior border of the ala orbitalis and the nasal capsule there is a comparatively small orbito-nasal fissure which is oval in form. In the model of the 19 mm. stage this fissure has become subdivided into two small openings, through the anterior of which the nasal nerve is transmitted.

The frontal bone curves around the basal margin of the ala orbitalis and extends along its orbital surface for some distance.

It is not possible to say exactly how the ala orbitalis was originally fused with the lamina trabecularis. Terry<sup>1</sup> described in the mesenchymal stage the ala orbitalis as being connected with the base of the skull, but the posterior root shows an interruption histologically. He describes the roots being formed as processes from the trabecular plate, naming the processes

<sup>1</sup> Terry, "Primordial Cranium of Cat," *Journ. Morphol.* 1917.



pre-optic and met-optic. Further, that these processes blend with corresponding processes of the ala, and that where the met-optic process joins with the post-optic root, there projects a processus paropticus, or processus orbitalis. The squirrel of the 17 mm. stage is too old to draw any conclusions as to the mode of union of the ala orbitalis with the lamina trabecularis. In *Tatusia novemcincta* at the 10 mm. stage, which would seem to correspond with the stage described by Terry of the cat, it would appear that the met-optic root, which alone is recognisable, is connected with the cornu trabeculae, but is not fused with it. The cornu trabeculae gives one the impression of giving off the ala hypochiasmatica which is connected with the rectus system of eye muscles in their earlier stages, but there is no sign of pre- and met-optic processes arising from the trabecular cornu. In *Tatusia* the term trabecular plate hardly holds, for it consists in the *Tatusia* of two cylindrical rods which lie side by side below the hinder part of the septum nasi and the interorbital septum. They diverge widely behind and do not form a trabecular plate, nor is that actually formed at the 12 mm. stage; in fact, if one use the term trabecular plate as being synonymous with lamina hypochiasmatica, it can scarcely be said to exist. Appearances suggest that in *Tatusia*, the pre- and met-optic branches of the apical part of the ala orbitalis grow down towards and fuse with the corresponding cornu<sup>1</sup> trabeculae.

#### LATERAL STRUCTURES

These include the ala orbitalis, the parietal plate and the supra-occipital cartilage, together with the commissures which connect these parts together. The ala orbitalis being connected with the central stem, has been described in the group of structures so classified.

The lateral wall of the nasal capsule might be included in this category or in the previous one, but it is, on the whole, more convenient to describe it with the nasal capsule as a whole, and it will only be introduced here to complete what may be alluded to as the cranial brim.

*Supra-occipital cartilage.* The supra-occipital cartilage unites with its fellow over the cavum cranii to form the tectum cranii posterius. It spreads in a downward direction to unite with the hind end of the ex-occipital cartilage opposite the dorsal prominence of that cartilage (Pls. I, II). It spreads upwards and forwards to unite with the parietal plate in a narrow occipito-parietal commissure; medialwards, as has before been mentioned, it meets its fellow in the middle line forming an unusually deep tectum posterius.

*The parietal plate* (Pl. III). This plate, otherwise, lamina supra-capsularis, is attached by a broad anteroposterior root to the anterior half of the upper border of the pars canalicularis. It may be described as rising almost vertically with a slight inclination lateralwards. It divides into a posterior part and an anterior part. The posterior part rises up and spreads backwards, becoming confluent with the supra-occipital cartilage, through the occipito-parietal

<sup>1</sup> Cornu is used here to express the hinder divergent extremity of the trabecula.

commissure. The anterior part passes forwards and soon splits into upper and lower branches. The lower branch, which is of considerable depth, comes to an end very soon. The upper branch is continued forwards to the posterior basal angle of the ala orbitalis with which it is fused. To the outer side of both divisions of the parietal plate, lies the parietal bone.

NASAL CAPSULE (Pls. I, II, III, IV, fig. 1)

The nasal capsule is comparatively short from before backwards, and when viewed from above, presents three segments; a posterior segment which is the pars posterior, an intermediate segment, the pars intermedia and an anterior segment, the pars anterior. These segments are separated by grooves or sulci from each other. Thus the pars posterior is separated from the pars intermedia by the postero-lateral sulcus which corresponds with the main root of attachment of the first primary ethmo-turbinal. The pars intermedia is bounded in front by the sulcus antero-lateralis which separates it from the pars anterior. At least one third, and that the hinder third of the dorsal aspect of the nasal capsule opens at this stage into the cranial cavity by means of two large openings separated by the septum nasi. This is the sub-cerebral part of the capsule. The remainder is pre-cerebral. The sub-cerebral part of the capsule shows, as before said, two large openings into the cranial cavity and there is, as yet, no sign of a lamina cribrosa. The caval orifices, which are separated from one another by the upper margin of the septum nasi, are ovoidal in form. Each is bounded medially by the septum, laterally by the upper margin of the frontal prominence of the pars intermedia and the upper margin of the pars posterior. Posteriorly the opening is bounded by the anterior margin of the tectum nasi posterius, otherwise the tectum cupulae. Each caval orifice is divided into two main bays by the dorsal edge of the first primary ethmo-turbinal, which is directed from behind, forwards and inwards towards a backward projection from the crista galli of the septum. The antero-lateral bay leads into the interior of the frontal recess of the pars intermedia and transmits the antero-lateral bundle of olfactory nerves. The postero-median bay is, in the main, connected with the pars posterior. It transmits the postero-median group of nerves to that region. It is divided into two smaller bays by the projection into it of the second primary ethmo-turbinal.

The orbito-parietal commissure is attached to the middle third of the lateral margin of the caval orifice.

*The pre-cerebral part of the nasal capsule.* This is made up of the pars intermedia and pars anterior. It is almost symmetrically divided by the sagittally directed sulcus dorsalis nasi which, commencing in front, reaches the whole length of the pars anterior but spreads out and is lost in the pars intermedia. The pre-cerebral part is widest opposite the most anterior part of the pars intermedia. In front of this, it narrows somewhat; then again widens out, and remains of considerable width to its termination. In the pars intermedia, near the middle line and on each side of the middle line is a wide

slit-like opening which is the foramen epiphaniale for transmission of the nasal nerve. Anteriorly the pars anterior terminates on each side in an imperfect cupula anterior.

*Lateral aspect of the nasal capsule.* The lateral aspect shows the three primary divisions of the capsule separated by the delimiting sulci.

The *pars posterior* narrows behind to form the cupula posterior. Its upper margin is attached to the anterior division of the pre-optic ramus of the ala orbitalis. In front of this attachment, the upper margin of the pars posterior is free, forming the lower boundary of the orbito-nasal fissure. In front of this, it is attached to part of the orbito-parietal commissure. The inferior margin of the pars posterior is free and in its posterior half or so is incurved to form the lamina transversalis posterior. As to whether or no this segment develops independently, as has been shown to be the case in the cat (Terry), in the mole (Noordenbos) and in the calf (own collection), cannot be even surmised from the stage now being described.

*Pars intermedia.* This forms the deepest part of the lateral wall of the capsule. It juts out between the antero-lateral and postero-lateral sulci. It is readily subdivisible into an upper larger and a lower smaller prominence by a sulcus which coincides with the course of the first part of the naso-lacrimal duct. The frontal prominence gives attachment to the anterior extremity of the orbito-parietal commissure. It corresponds with two recesses in the interior of the nose, viz. the recessus frontalis and the recessus anterior, but the recessus anterior does not give rise to any separate prominence, such as may be seen in many mammals. The inferior prominence or prominentia maxillaris is not so large as the frontal prominence and owes its existence to the recessus maxillaris. From this prominence the inferior oblique muscle of the eyeball takes origin. The prominentia maxillaris when traced forwards spreads out into a triangular flattened area contained between the limbs of bifurcation of the sulcus antero-lateralis. The area is the lamina supra-condialis and it corresponds with the recessus glandularis on the medial aspect. Lateral to it lies the naso-lacrimal duct.

The pars anterior, as seen from the side, is of triangular form, the apex being directed backwards to the medial side of the foramen epiphaniale. Its lower side lies in front of the main upper stem of the sulcus antero-lateralis and the lower of the two branches into which it divides. Towards its anterior end the lower side is fused with the lamina transversalis. Anteriorly, the site of fusion is indicated by a deep sulcus as seen from below, but as viewed from the interior of the nasal capsule corresponds with the atrio-turbinal. The upper side of the pars anterior blends with the tectum nasi at a rounded border. The basal border corresponds for the most part with the lateral margin of the fenestra narina anterior. This, where it joins the lower border in front of the lamina transversalis anterior, is continued into a wing-like process, the processus alaris superior, but above this process the basal border is inrolled to form the margino-turbinale.



*Fenestra narina.* The fenestra narina is conveniently divisible into a larger dorsal segment, and a smaller ventral segment. The two lie nearly at right angles with one another, the plane of the former being almost coronal with a slight lateral backward tilt, that of the latter being horizontal. The larger upper part has been named by Terry the pars atrialis, and the lower part has been named by him the pars lacrimalis, because it is through the most posterior and external part of this segment that the naso-lacrimal duct enters the nasal cavity. The two segments are almost completely separated from one another by processes which spring from the medial (anterior) and lateral (posterior) margins of the main orifice. The process which springs from the medial wall may be spoken of as the inferior cupular process; the one from the lateral wall is the superior alar process. Although conditions are very much modified in man, owing specially to the shortening of the pars anterior, it is possible that this process may be represented in man by the crus mediale of the alar cartilage. The upper segment may be looked upon as a perforation in a cupula anterior which is unusually complete, and which forms the medial and superior boundaries of the aperture. The lateral boundary is inrolled about its middle to form the margino-turbinal. The lacrimal segment of the fenestra is bounded on its medial side by the processus lateralis ventralis of the septum. Posteriorly it is bounded by the lamina transversalis anterior. Externally it is bounded by the inferior margin of the paries nasi, and in its outermost part is lodged the naso-lacrimal duct.

*The solum nasi.* The solum nasi is in comparison with that of other mammals, fairly complete. It is represented by the lamina transversalis anterior, and the lamina transversalis posterior, as well as by the common paraseptal cartilage which extends between the two. Of these parts, the least complete, as far at least as chondrification is concerned, is the lamina transversalis posterior. In the solum nasi is the large antero posteriorly elongated fenestra basalis, which is separated from the lacrimal segment of the fenestra narina by the lamina transversalis anterior. The lamina transversalis anterior connects the lower wall of the pars anterior with the septal wall. The actual connection with the septal wall is very slight and one might even describe it as being connected with the septal wall through the hinder end of the processus lateralis ventralis. It is obliquely inclined so that the outer extremity is at a higher level than the inner extremity. The former is also much narrower than the latter, being reduced in width through the presence of an incisura pre-transversalis and an incisura post-transversalis. It is through the incisura pre-transversalis that the lacrimal duct enters the lacrimal segment of the fenestra narina. The inner extremity of the lamina transversalis is much wider than the outer, and that is due to increase in length of the internal posterior basal angle in a backward direction, towards the anterior extremity of the common paraseptal cartilage, with whose medial lamella it is more particularly united. The anterior border of the lamina transversalis is practically straight and transverse. The posterior border is very oblique running

backwards and inwards at about an angle of  $45^\circ$  with the anterior border. Not only does the lamina pass in a backward direction; it also passes downwards, and it fuses at an obtuse angle with the medial lamella of the common paraseptal cartilage. The greater part of the lamina is separated from the septum nasi by a fissure. Only a very narrow connection is formed between the lamina and the septum and that at the antero-internal angle. At the junction of the lamina transversalis with the paries nasi it is crossed by the naso-lacrimal duct which is lodged in a sulcus formed by the upbending of the junctional region. This upbending produces, in the interior of the nose, the atrio-turbinal.

*Lamina transversalis posterior.* This is the floor of the cupula posterior of the lateral nasal capsule. It is imperfectly chondrified at this stage, but is connected by its front edge with the common paraseptal cartilage. It is entirely free of the septum.

The *common paraseptal cartilage* stretches between the laminae transversales anterior and posterior. It consists of two parts, an anterior which is in the form of a vertically disposed curved plate in whose concavity is lodged the organ of Jacobson, and a posterior which is a cylindrical rod-like structure. At the anterior extremity of the common paraseptal cartilage a very short tunnel is formed by a bridge connecting the extremities of the curved plate around the duct of the organ of Jacobson. The convex side of one paraseptal cartilage almost meets that of the opposite cartilage below the region of the septum. The more posterior cylindrical segment of the common paraseptal cartilage is related to the vomer which lies on its medial aspect. It is this part of the common paraseptal cartilage which is the first to fail to chondrify in those animals in which the solum nasi is less complete than in the one under consideration. The common paraseptal cartilage is separated from the septum in its whole length by the septo-paraseptal fissure.

*Medial aspect of the lateral wall of the nasal capsule* (fig. 2). This consists, like the lateral aspect, of three parts, namely, pars anterior, pars intermedia and pars posterior. The pars anterior is limited behind by the main limb of the crista semicircularis and by the downward continuation of its anterior limb of bifurcation. Anteriorly, it reaches the lateral margin of the pars atrialis of the fenestra narina.

The pars intermedia is bounded in front by the crista semicircularis, and by the anterior of the two limbs into which it bifurcates, while posteriorly, it is limited by the root of the first primary ethmo-turbinal, but above the level of this root, it communicates with the cavum cranii, by the antero lateral bay of the caval orifice (fenestra olfactoria of Terry). It represents the deepest part of the nasal capsule.

The pars posterior may be described as being bounded in front and above, by the free edge of the first primary ethmo-turbinal. It is bounded behind by the roof, the posterior wall and floor of the cupula nasi. It is characterised by the presence of turbinals. In this particular instance there project into it the second ethmo-turbinal and above that the medial lamella of bifurcation of

the first ethmo-turbinal. The pars posterior is in free communication with the cavum cranii at this stage through the postero medial bay of the fenestra olfactoria. It is the meatus between the second and first ethmo-turbinals in particular which communicates with the caval orifice. No other turbinal is developed in this region at this time. These parts may now be described in greater detail.

The *pars anterior* is divisible into two definite regions, viz. an anterior or atrial region, and a posterior divisible into an upper and a lower channel by means of a ridge which is the naso-turbinal.

The lower channel is continuous posteriorly with the recessus glandularis of the *pars intermedia*. The upper channel is limited sharply behind by the

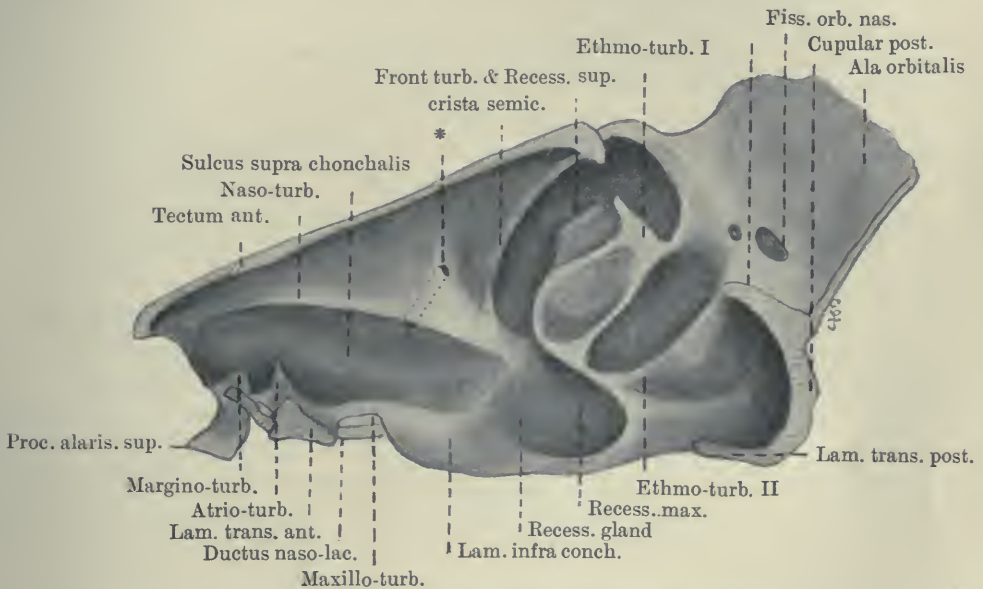


Fig. 2. *Xerus*. Medial aspect of lateral wall of nasal capsule.

stem of the crista semicircularis and into its hinder part opens the foramen epiphaniale. The naso-turbinal is for the most part in continuity with the lateral cartilaginous wall, but towards its hinder end a tunnel passes underneath it and separates it from the lateral wall. Below the naso-turbinal there runs a wide channel which is bounded inferiorly by the atrio-turbinal and by the lamina transversalis anterior. It may be called the supra conchal meatus.

The *pars intermedia* is deeply recessed between the root of the first primary ethmo-turbinal and the stem of the crista semicircularis. It is especially deep in its upper half or three-quarters. In its lower third or half it becomes shallower in a forward direction, forming a recessus glandularis which anteriorly communicates with the supra conchal meatus, and posteriorly opens into the deeper recessus maxillaris. Perhaps its most anterior inferior part may be



regarded as being formed by the maxillo-turbinal, in front of which there is a deep post-transverse notch. The upper part of the pars intermedia whose floor is formed by the upper half of the first primary ethmo-turbinal is the recessus frontalis, which is complicated by the presence in it of a frontal turbinal. This recess opens into the cavum cranii through the antero-lateral bay of the fenestra olfactoria. The lower part of the upper segment of the pars intermedia projects forwards under cover of the lower part of the stem of the crista semicircularis to form the recessus anterior.

*Pars posterior.* The pars posterior, which is bounded in front by the free edge of the first primary ethmo-turbinal, is divided into two main parts by the projection of the second primary ethmo-turbinal. That part which lies above and in front of the second primary ethmo-turbinal is in free communication with the postero-median bay of the fenestra olfactoria. It is complicated by a secondary turbinal which is given off from the medial aspect of the first primary ethmo-turbinal. The lower division is practically the cavity of the eupula and it is not in free communication with the cavum cranii as it is separated from it by the roof of the eupula.

#### STRUCTURES FORMING THE VAULT AND CRANIAL BRIM

The *cranial vault* is formed by a large broad and deep tectum, which runs very straight across from side to side. By means of three processes the tectum was connected laterally with other parts of the cranium. By its lowest process it is fused, without histological distinction with the ex-occipital; by the middle very small process, it is attached to the pars canicularis of the auditory capsule; by its uppermost process, it is connected through the occipito-parietal commissure with the parietal plate. The middle or occipito-capsular commissure, formed by the middle process just described, divides what would otherwise be a long curved occipito-capsular fissure, into an upper and a lower segment. The lower margin of the tectum shows a wide and fairly deep notch, the incisura superior.

The *cranial brim* is formed in the following way: in front by the anterior margin of the fenestra olfactoria; then by the spheno-ethmoidal commissure, behind which comes the ala orbitalis. This is followed by the orbito-parietal commissure and this in turn by the parietal plate. This latter is continued backwards by the occipito-parietal commissure into the supra-occipital cartilage which forms one half of the tectum posterius. The structures above mentioned constitute one half of the cranial brim.

The *naso-lacrimal duct* (Pl. III) commences by the fusion of two canaliculi opposite the sulcus which, on the outer aspect of the lateral wall of the capsule, divides the prominentia frontalis from the prominentia maxillaris. It continues along the lateral wall near its lower margin occupying the sulcus maxillo-conchalialis until it reaches the lamina transversalis anterior; it then passes across this near its junction with the paries nasi, producing a sulcus whose upper convexity projects as the atrio-turbinal. In front of the lamina trans-

versalis anterior the naso-lacrimal duct enters the nose and is confluent with the nasal mucosa.

*Visceral skeleton* (Pl. III). The visceral skeleton of the first arch is represented by Meckel's cartilage and its two posterior derivatives, the malleus and incus. Meckel's cartilage is long, cylindrical, circular in section in its anterior fourth, and oval in section with the long axis vertical about the middle. Just before it merges with the malleus cartilage it becomes oval. The malleus cartilage is somewhat remarkable in that it is prolonged backwards over the incus into a deep recess under the tegmen tympani. The handle runs parallel with Meckel's cartilage and, like it, is therefore directed inwards. It almost touches the cochlear capsule opposite the sulcus septi. The incus cartilage is, perhaps, in comparison with the malleus cartilage, unduly small. Its processus brevis is not lodged in any fossa incudis, but rather rests against the basal aspect of the pars canalicularis. The processus longus is articulated in the normal way with the head of the stapes cartilage. The stapes cartilage is of much the usual form. It transmits the stapedia artery and is fitted by its foot-piece into the fenestra vestibuli. This fenestra is much larger than the foot-piece of the stapes at this stage.

*Cartilage of the second arch.* This is represented by a cartilage reaching continuously from the crista parotica to the junction of the corpus hyale with the thyro-hyale. Beyond being cartilaginous in its whole length it calls for no comment. No sign of ossification is present.

The cartilage of the third visceral arch (thyro-hyale) is short and directly connected dorsally with the superior cornu of the thyroid cartilage. Anteriorly it passes without histological differentiation directly into the corpus hyale.

The cartilage of the fourth arch, namely, the thyroid cartilage, is at this stage confluent with its fellow of the opposite side. From the extremities of its posterior border cornua project, namely a superior cornu which is confluent with the posterior end of the thyro-hyal cartilage. Just in front of this posterior border and lying parallel with it foramina are found. There are as many as four in the 17 mm. stage. It is of interest that there should be so many for it puts entirely beyond the range of possibility the supposition that the thyroid cartilage is the result of fusion of two or more visceral arches. The author has long ago pointed out that the thyroid cartilage from *Metatheria* onwards is derived from the fourth visceral arch.

Towards the middle line the thyroid cartilage presents some peculiarities. There is no sign of a superior median notch. The two alae of the thyroid cartilage are of considerable depth, but at this stage they are not fused for more than the upper half of what would be the medial border in the unfused condition, and from the lower border of the plate formed by the fusion of the two alae there descends a long median process of cartilage which separates for a considerable distance the two alae from one another. Below this process the alae approach each other so closely as to be separated by little more than a fissure, and it is interesting to note that in a later stage, namely 19 mm. the

alae have fused with this projection in such a way as to produce, in the thyroid cartilage, two foramina lying on either side of the middle line.

The cartilage of the fifth arch, namely the cricoid, does not show anything worthy of comment. It is completely ring-like.

#### THE OSSEOUS SKELETON (Pl. IV)

*Parietale.* The parietale is well ossified as a membrane bone and it covers the upper half or so of the parietal plate. It narrows when traced forwards and finally overlaps the lower posterior angle of the frontale, which it much resembles in general outline.

The *Frontale* is a larger bone than the parietale but like it is broad behind and somewhat narrow in front. It covers the ala orbitalis in part and the sphenothmoidal commissure and prominentia frontalis of the pars intermedia of the nasal capsule. An orbital plate is formed but is in a comparatively rudimentary form.

The *Incisivum* consists of facial and alveolar parts. The facial part extends upwards by the side of the pars anterior of the nasal capsule, as well as medially under the lamina transversalis anterior and the naso-lacrimonal duct. There is no sign of a septomaxillary bone, nor is there as yet any sign of a paraseptal process (praevomer) of the incisivum.

The *Maxilla* shows a body which lies lateral and inferior to the prominentia maxillaris of the nasal capsule and from which there projects upwards a frontal process parallel with the ascending process of the incisivum. From the body there projects inwards under the nasal capsule a large palatine process. An infraorbital foramen, which is very large and resembles that found in *Microtus* in being long, narrow and comma shaped, is present. The outer wall of this foramen is formed by a slender bar of bone which stretches from the posterior aspect of the frontal process downwards to the zygomatic bone and is then tied to the body of the maxilla by a slender bar. No sign of accessory cartilage was noted in any part of the maxilla.

*Palatinum.* This is a small curved plate-like bone lying behind the maxilla from which it is separated by a considerable interval. It is placed in front of the outer end of the processus alaris of the intermediate region of the central stem.

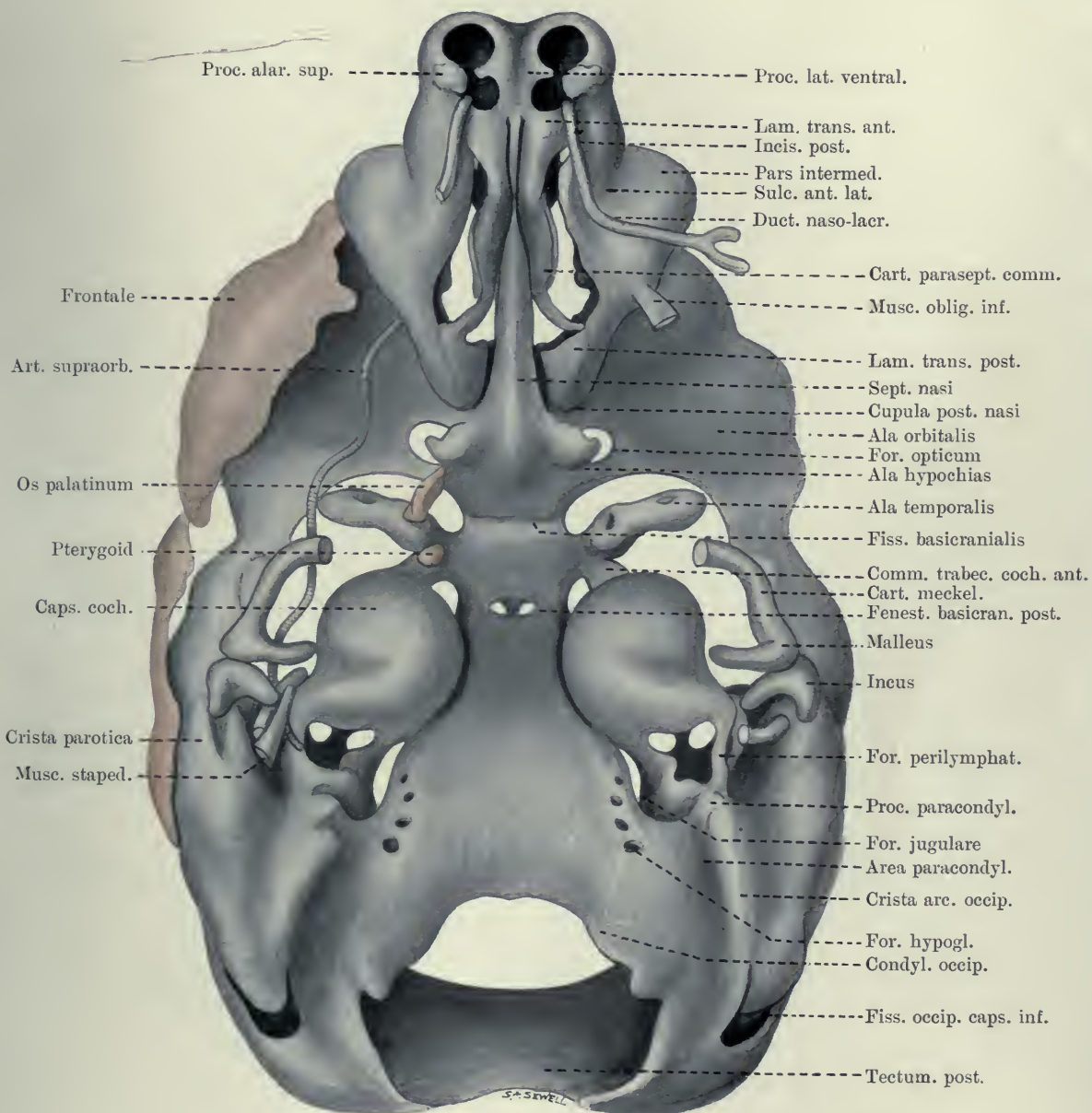
The *Pterygoid* lies medial to the ala temporalis and behind the palatinum. It practically rests against the cochlear capsule which is of moderate size.

*Zygomaticum.* This is a slender bone interposed between the maxilla and squamosum. It does not reach the maxilla in front nor is it in contact with the squamosum, but passes below the anterior end of the squamosum.

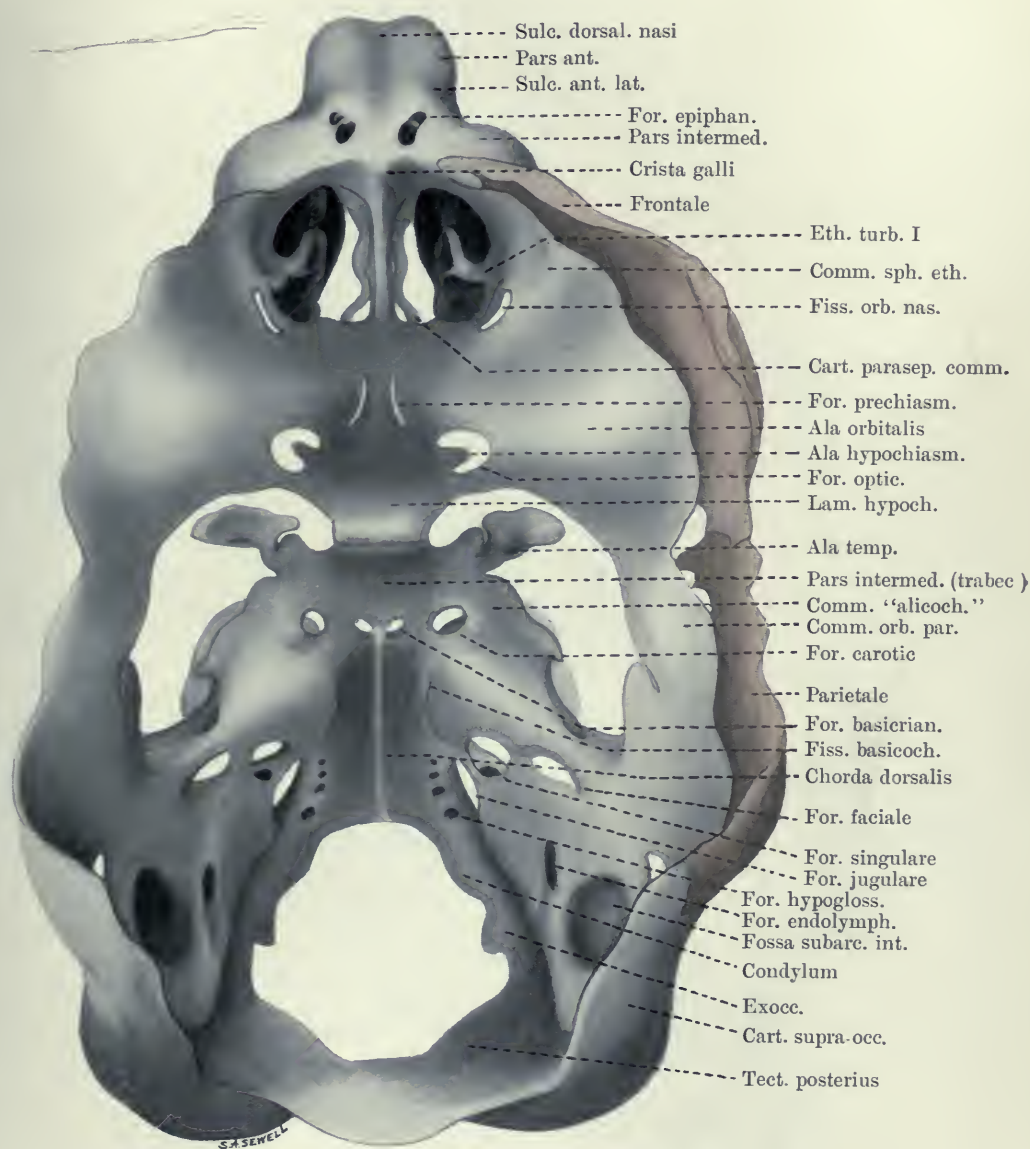
The *Squamosum* in its posterior half or so lies lateral to the malleus cartilage. It has no relation whatever to the incus which is perhaps somewhat unusual. Anteriorly the squamosum bends downwards to lie over the hinder end of the zygomaticum.

The *Mandibula* consists at this stage of a long slab of bone extending from



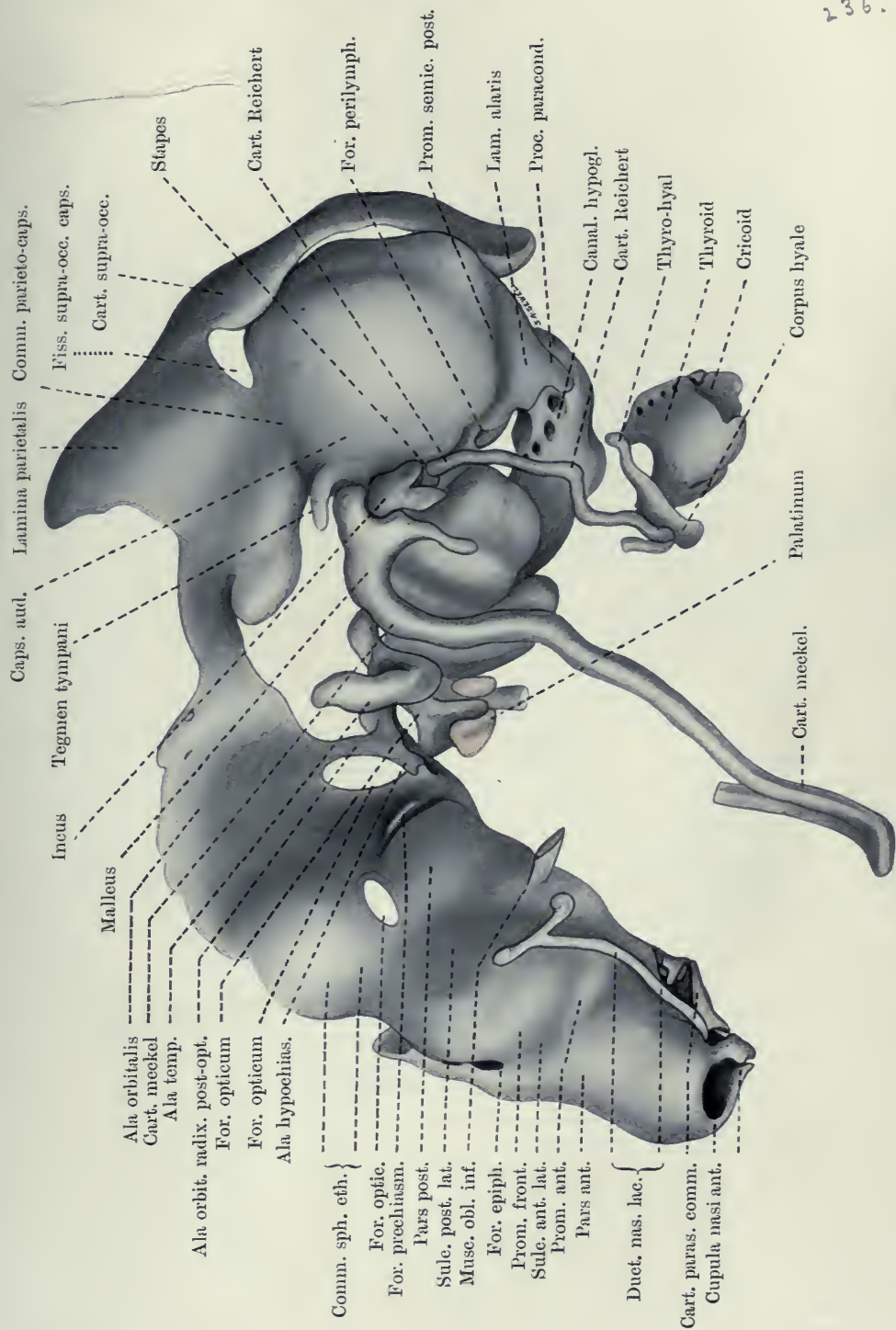






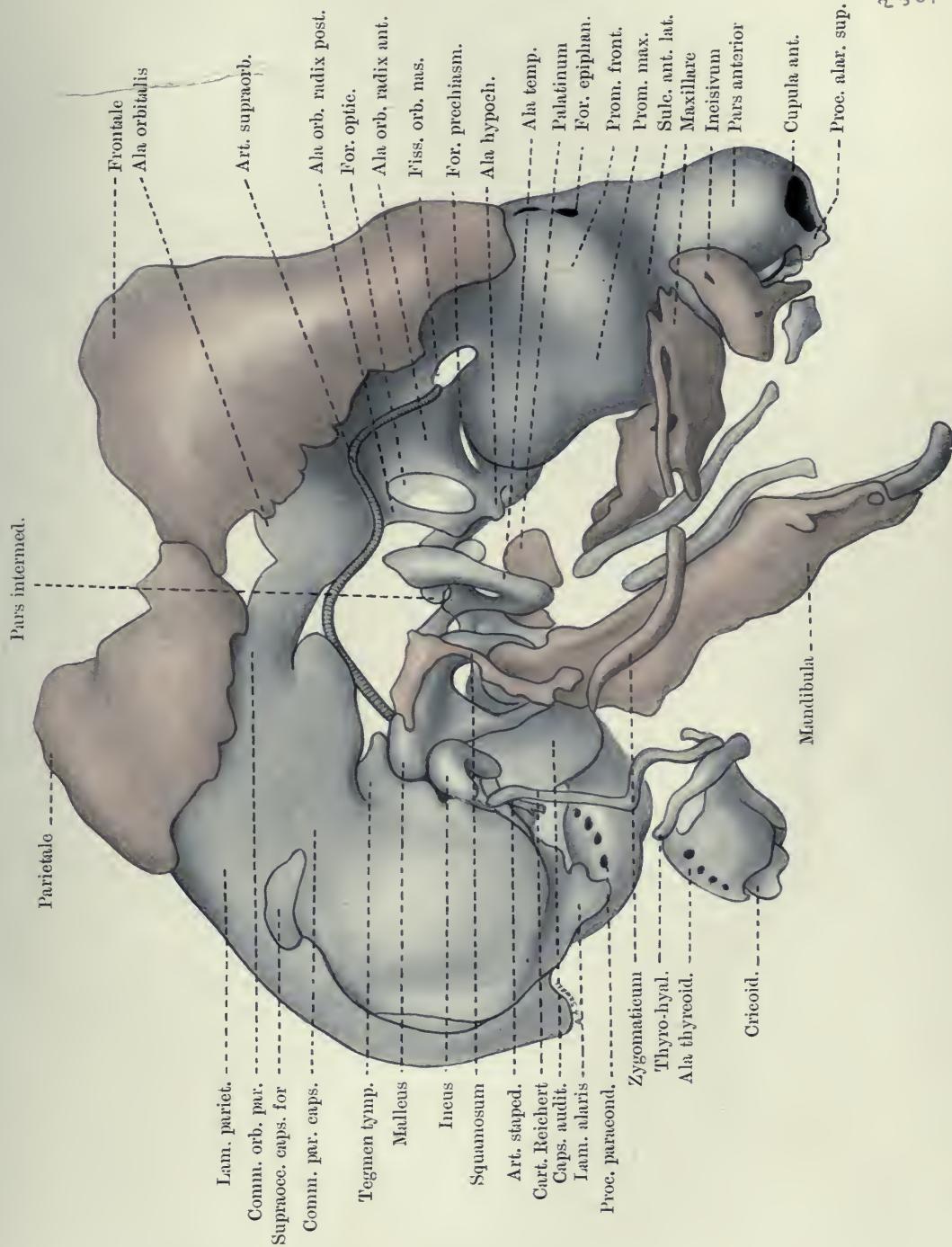














near the handle of the malleus cartilage to a point not far behind the fused anterior extremities of Meckel's cartilages. The anterior extremity is much narrower than the rest of the bone and does not hide Meckel's cartilage when viewed from the side. A small internal or alveolar wall is present and overhangs Meckel's cartilage. It lies opposite the middle of the mandible. At this early stage neither the lacrimal nasal, tympanic, praevomer nor vomer is ossified but at the 19 mm. stage the vomer is present and is of considerable size. It consists of two separate pieces placed between the cylindrical posterior parts of the common paraseptal cartilages. It may be said in passing that at the 19 mm. stage the palatinum shows the palatine process which is not present at the 17 mm. stage.



## ON THE QUADRATE IN CRYPTOBRANCHUS, MENOPOMA, AND HYNوبيUS

By F. H. EDGEWORTH, M.D.

WIEDERSHEIM (1877) stated that in the adult form of *Cryptobranchus japonicus* s. *Megalobatrachus maximus* the quadrate has no basal articulation, but only a single dorsal union, and that the pterygoid process ends freely. Parker (1882) stated that the pedicle of the suspensorium (= basal process of the quadrate) passes into the basis cranii with which it is confluent, that the ascending process is continuous with the alisphenoidal wall, and the otic process with the auditory capsule. The "Epipterygoid" (= remains of the pterygoid process) forms a separate mass of cartilage lying in a groove in the pterygoid bone. The distal end of the "Stapes" was, on one side, confluent with the quadrate, on the other, articulated with it. "The epiphyal" was attached to the quadrate further down by ligamentous fibres.

I find in a 37 mm. larva (figs. 1 and 2) that the quadrate has cartilaginous pterygoid, ascending, basal, and otic processes. The pterygoid process passes forwards and its anterior end is confluent with the trabecula and with the inner end of the antorbital process. The ascending process is confluent with the crista trabecula. The otic process is confluent with the auditory capsule. The basal process is directed inwards and backwards and is confluent with the basiptyergoid process of the basal plate a little in front of the union of the latter with the auditory capsule. The columella auris passes from the fenestra ovalis on the outer wall of the auditory capsule forwards and slightly outwards and its anterior end is close to the posterior surface of the quadrate.

Wiedersheim stated that in the adult stage of *Menopoma alleghaniense* s. *Cryptobranchus alleghaniensis* the quadrate has an ascending process confluent with the alisphenoid, and a separated pterygoid process. Otic and basal processes are absent. Parker stated that in the adult state the quadrate has three processes, the ascending which passes into the alisphenoidal wall, the pedicle (= basal process) "which passes into the basis cranii above the angle formed by the divergence of the pterygoid and parasphenoid," and the otic which is confluent with the auditory capsule. The pterygoid process is a separate cartilage lying in a groove in the pterygoid bone.

I find that in a 20 mm. larva of *Menopoma* (fig. 3) the quadrate has no ascending, basal, or otic, processes. It has a long cellular pterygoid process which extends forwards from the quadrate to the trabecula. There is, as yet, no antorbital process. In a larva of 26 mm. (fig. 4) the quadrate has chondrified pterygoid, ascending, and otic, processes. The pterygoid process is confluent with the trabecula. There is no antorbital process. The ascending process is

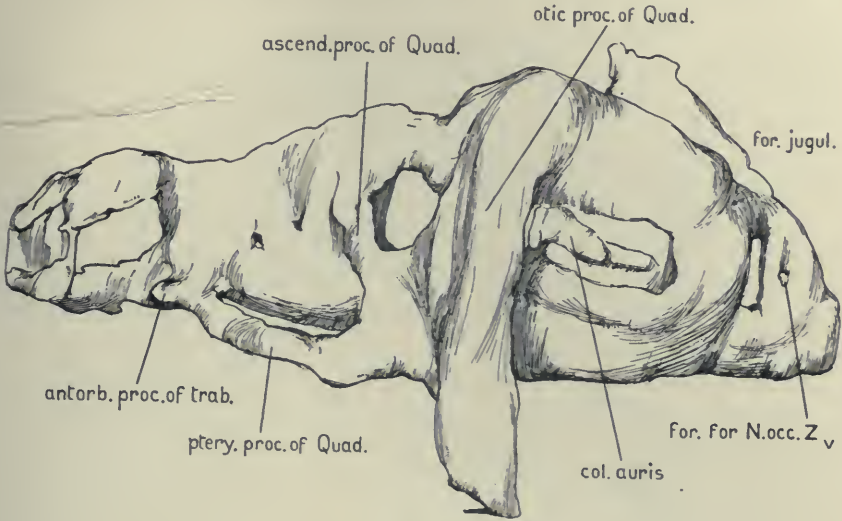


Fig. 1

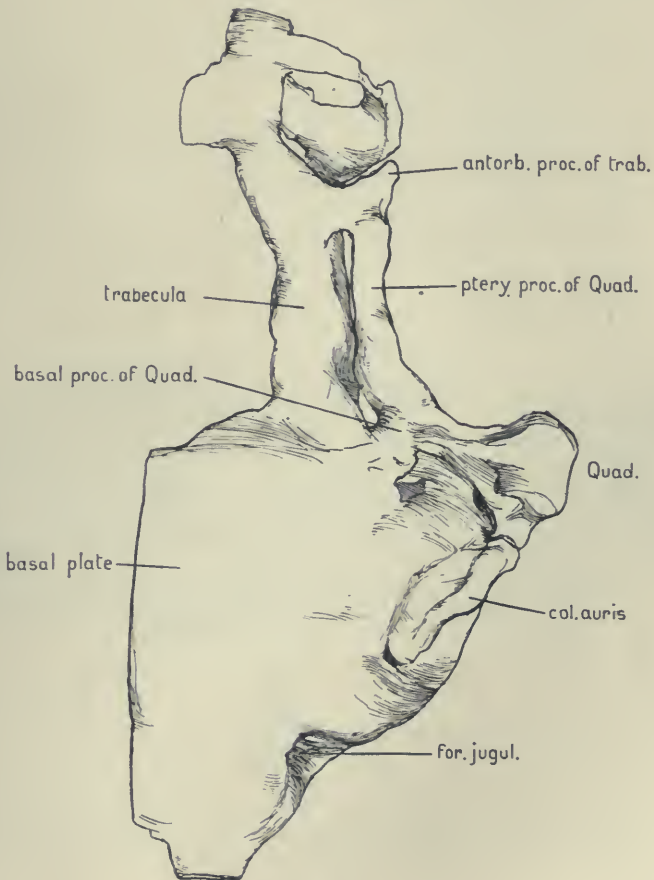


Fig. 2

Figs. 1 and 2. *Cryptobranchus*, larva 37 mm. Sketches of model of left half of chondrocranium.  
Fig. 1 from the side; fig. 2 from below.

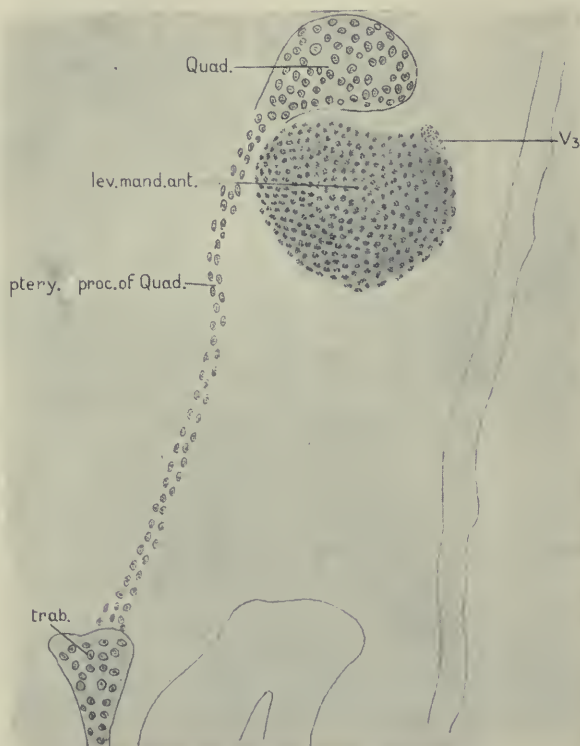


Fig. 3. *Menopoma* larva 20 mm. Horizontal section.

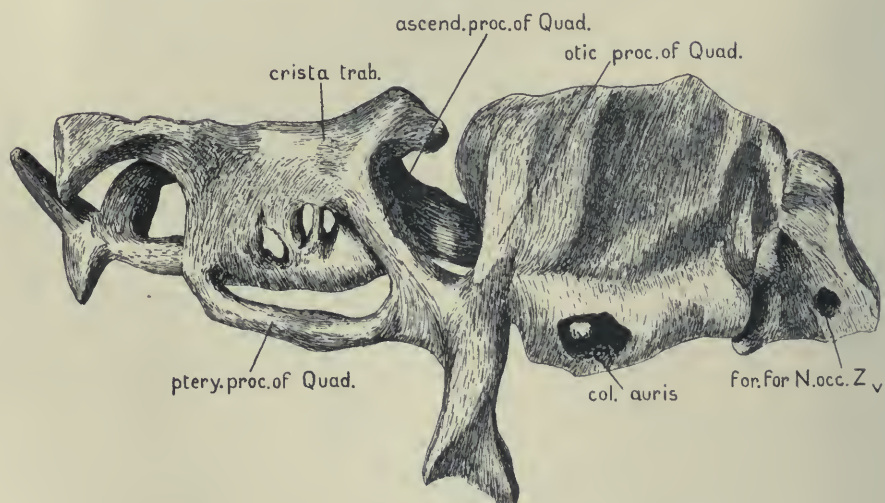


Fig. 4. *Menopoma* larva 26 mm. Sketch of model, from the side.



confluent with the crista trabeculae, and the otic process with the otic capsule. The crista trabeculae extends backwards beyond the upper end of the ascending process, but does not yet reach the auditory capsule. In a larva of 28 mm. (figs. 5 and 6) the antorbital process is developed; its inner part is confluent

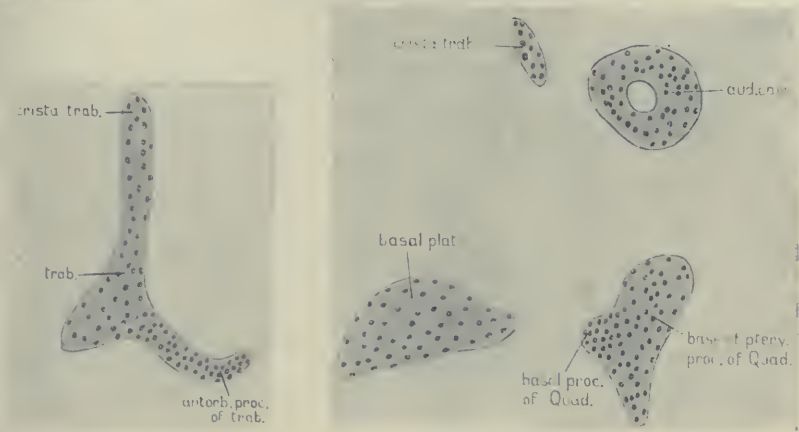


Fig. 5

Fig. 6

Figs. 5 and 6. *Menopoma* larva 28 mm. Transverse sections, fig. 5 through the antorbital process; fig. 6 through the quadrate and the inner end of its basal process.

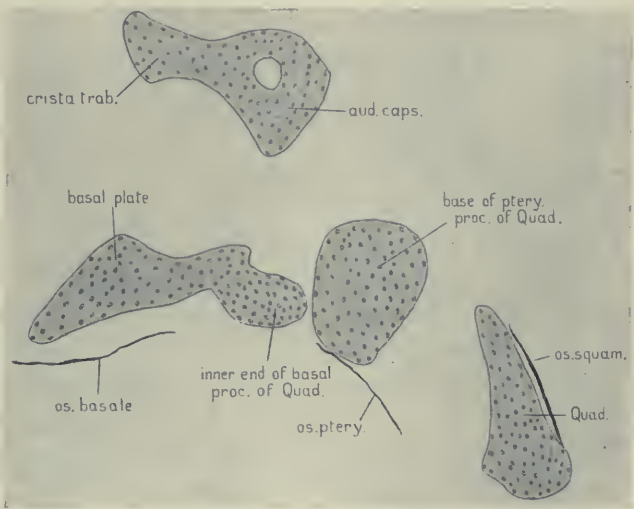


Fig. 7. *Menopoma* larva 40 mm. Transverse section through quadrate and the union of its basal process with the basal plate.

with the trabecula and with the inner end of the pterygoid process of the quadrate from which it extends antero-laterally. There is a slight basal process projecting from the base of the pterygoid process of the quadrate. The posterior end of the crista trabeculae is confluent with the anterior part

of the auditory capsule. In a 40 mm. larva (fig. 7) the basal process has extended inwards and backwards and its extremity is confluent with the outer part of the basal plate just in front of the junction of the latter with the auditory capsule. There is no basipterygoid process of the basal plate. The columella auris passes forwards and outwards from the fenestra ovalis, its anterior end is in contact with the squamous bone.

Wiedersheim stated that in the adult stage of *Hynobius naevius* s. *Ellipsoglossa naevia* a process of the quadrate passes towards and articulates with the basal surface of the prootic region. He did not mention the existence of



Fig. 8. *Hynobius* larva 13 mm. Horizontal section.

ascending, otic, or pterygoid processes, but in his figure depicts a pterygoid process which ends freely.

I find that in a 13 mm. larva of *Hynobius nebulosus* s. *Ellipsoglossa nebulosa* (fig. 8) the quadrate has ascending, otic and pterygoid processes. The ascending process is confluent with the crista trabeculae, and the otic process with the auditory capsule. The pterygoid process is wholly cellular; its anterior end is continuous with the trabecula. The antorbital process has not yet developed. In a larva of 20 mm. (figs. 9, 10 and 11) the ascending process is confluent with the crista trabeculae and the otic process with the auditory capsule. The pterygoid process is wholly chondrified; its anterior end is confluent with the trabecula and with the inner end of the antorbital process which has now

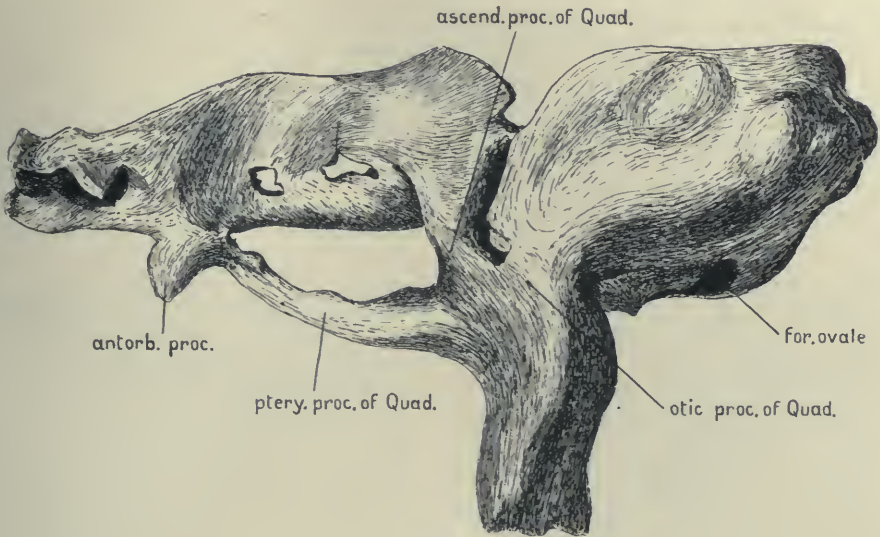


Fig. 9

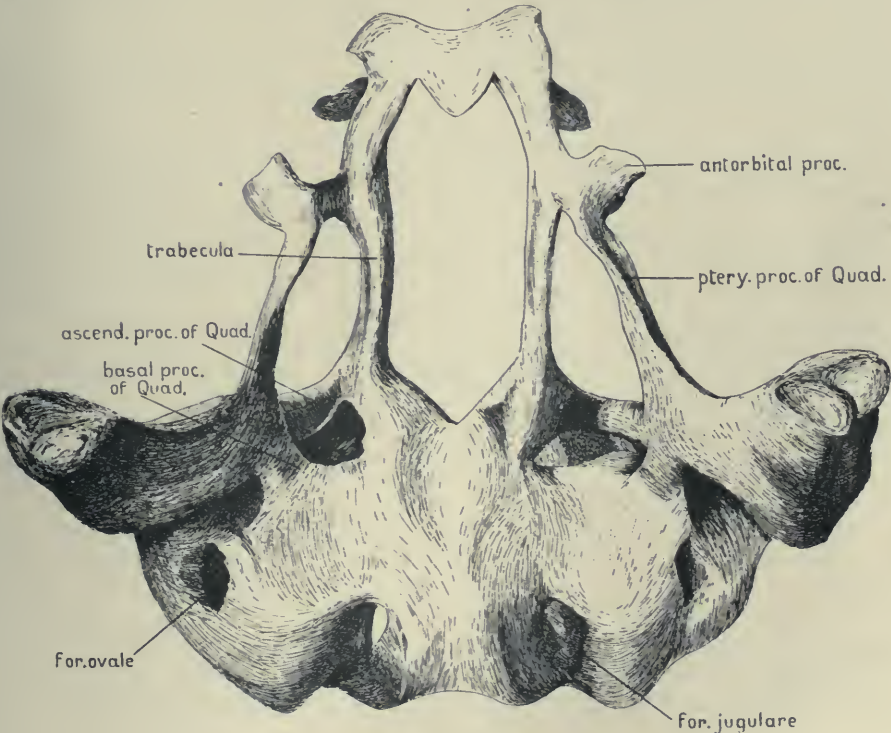


Fig. 10

Figs. 9 and 10. *Hynobius* larva 20 mm. Sketches of model, fig. 9 from the side; fig. 10 from below.



developed. The basal process has developed and chondrified; its inner end is confluent with the base of the auditory capsule. The columella auris is not yet developed. In a larva of 37 mm. (fig. 12) and in the adult stage, the anterior part of the pterygoid process has disappeared, and a syndesmotie joint has developed between the basal process of the quadrate and the base of the auditory capsule. The ascending and otic processes are continuous with the crista trabeculae and with the auditory capsule respectively.

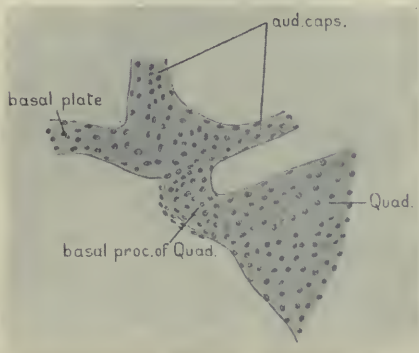


Fig. 11. *Hynobius* larva 20 mm. Transverse section through quadrate and its basal process.

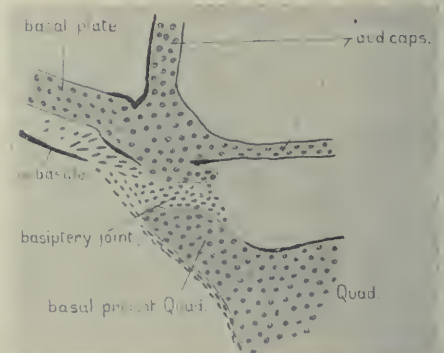


Fig. 12. *Hynobius* larva 37 mm. Transverse section through basiptyergoid syndesmotie joint.

As regards the quadrate, there is a greater similarity between *Cryptobranchus* and *Menopoma* than between either of them and *Hynobius*. In the two former the ascending process passes upwards and forwards from the base of the pterygoid process, whilst in *Hynobius* it passes nearly vertically upwards from the body of the quadrate. In a future paper I hope to discuss the phylogenetic significance of these and of some other phenomena in Amphibia.

I have the pleasure of thanking Prof. J. P. Hill for the loan of the larva of *Cryptobranchus*, and Prof. Watasé for the larvae of *Hynobius*. Figs. 1 and 2 were drawn by Miss Cross, figs. 4, 9 and 10 by Miss Harvey.

The expenses of the investigation have been defrayed by the Bristol University Colston Society.

Sept. 14, 1922.

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# SOME OBSERVATIONS ON THE ROOF OF THE PRIMORDIAL HUMAN CRANIUM

BY PROFESSOR FAWCETT, M.D.

IT has been the custom for some time to accept the views expressed by Bolk (*Petrus Camper*, 2 Deel, pp. 315 etc.) which were based on results obtained from specimens stained in bulk by Van Wijhe's bulk stain and differentiated.

By this method results were obtained so much at variance with what obtains in vertebrates other than man, and so different from anything obtained in the usual way in man, that in 1910 I ventured to say: "I must confess the appearances in his figures scarcely explain what is seen in this cranium." Macklin in 1921 in a description of "The skull of a Human Fetus of 43 millimetres greatest length," is more precise and states that Bolk has been led into quite a number of errors through the method used. It is only fair to say that Bolk himself does not place implicit faith in the methods, for he says on p. 322, "In der mitte der occipitalregion bleibt unterhalb des Knorpelringes ein Feld übrig das nicht knorpelig verschlossen wird, *wenigstens das von mir angewendete Verfahren ist nicht in Stande einen vollkommenen knorpeligen Verschluss ans Licht zu führen.*" (The italics are mine.)

Bolk illustrated his communication by four coloured figures which represent different ages in sequence. In fig. 1 one sees from below upwards, cartilage centres in the cervical vertebrae, separate on the two sides but connected together dorsally by a spinal membrane; above the vertebrae on each side one sees cartilage in a somewhat broad sheet forming what appears to be the side of a foramen magnum, and connected together about their middle by a narrow bar of cartilage from which a small process ascends. Below this bar is an uncoloured area, Bolk's spino-occipital membrane, which is continuous with the spinal membrane below and contains two small nodules of cartilage. Above the transverse bar above mentioned is a transversely placed separate mass of cartilage.

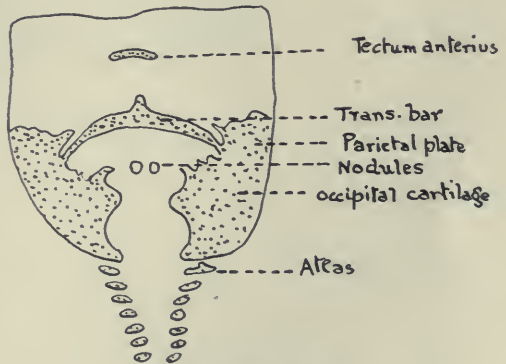


Fig. 1 (after Bolk).

Bolk regarded the spino-occipital membrane as reaching up to the transverse bar of cartilage which connects the two side walls of cartilage together,

and he rightly said that this transverse bar has nothing to do with bounding the foramen magnum. He did not actually realise that the conditions appearing in his specimen are entirely due to the method used, for all that part lying between the two small nodules and the transverse bar of cartilage is actually cartilage undergoing calcification and therefore has lost its stain during differentiation unless perchance it never was stained. Hence the upper segment of the spino-occipital membrane is non-existent.

It is hoped that this communication will show that there are in reality three tecta in the vault of the cranium, which may be named from behind forwards tectum posterius or tectum occipitale, tectum intermedium or tectum parietale posterius and tectum anterius or tectum parietale anterius.

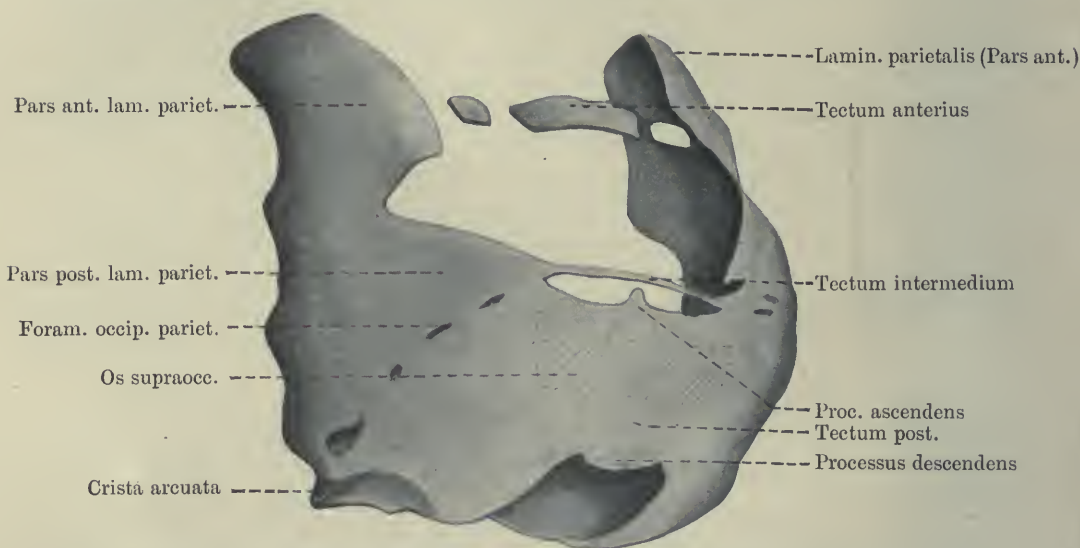


Fig. 2. A combination of appearances at about 30 mm. C.R. length. Human, viewed from behind.

Text fig. 2 shows the condition of affairs in the chondro-cranium at about the 27 millimetre crown-rump stage. The tectum posterius is seen as a broad band connecting the occipital cartilages above the foramen magnum; from its upper border in the mid-line a short ascending process projects and a broader but short process projects downwards—the processus descendens. These processes were described by me in 1910. Laterally the tectum merges into the corresponding supraoccipital, which is separated incompletely from the parietal plate by an oblique row of unchondrified areas usually associated with the auditory capsule. These areas appear as foramina in the model. They lie along the occipito-parietal groove of Macklin. If they be followed up they lead to a notch situated in the upper edge of the wall of cartilage formed by the supraoccipital cartilage and the parietal plate—Macklin has named this notch the incisura occipito-parietalis. Anterior to the supraoccipital cartilage is the parietal plate (lamina parietalis or lamina supracapsularis). This I think



should be described as consisting of an anterior and a posterior part separated by a deep notch. The posterior part is directed upwards and inwards above the outer edge of the supraoccipital cartilage. It either ends freely or is connected with the corresponding spot on the opposite side by a narrow bridge of cartilage—the tectum intermedium or parietale posterius. This tectum has only a very short life. It is not present at the 27 mm. stage and it has disappeared at the 32 mm. stage. It does not take part in the formation of the interparietal bone and it is not brought out in any of Bolk's figures.

The anterior part of the parietal plate varies somewhat in form with age but is well developed at the 30 mm. stage. As it rises in the cranial wall it broadens antero-posteriorly and posteriorly is prolonged as a short angular projection. Stretched between these posterior processes is a chain of three pieces of cartilage, viz. a median and two lateral; these constitute the tectum antierius or tectum parietale antierius.

The two lateral pieces disappear before the 48 mm. stage, but at this stage the median piece still persists. The tecta are thus:

- (a) Tectum occipitale or posterius.
- (b) Tectum parietale posterius or tectum intermedium.
- (c) Tectum parietale antierius or tectum antierius.

So far as I know only the tectum posterius is converted into bone. Macklin shewed that at the stage described by him, viz. 43 mm., there was an area of calcified cartilage in the occipital tectum and the adjacent supraoccipital cartilages which assumed the form of a butterfly with outstretched wings. In my own specimens at the 27 and 32 mm. stages the same thing occurs. In fig. 2 the calcified area is shown. This area is the area which Macklin has stated is calcified and therefore has either not stained or has lost the stain during differentiation.

It is easy to see that if the stain were lost from this area two cartilaginous bars would appear to cross the mid-line from side to side and that from the upper bar a processus ascendens would project upwards and from the lower a processus descendens would project downwards into the foramen magnum. The bars would appear to be separated by a clear unstained area, which Bolk thought to be unchondrified. Further as age advances two important changes occur. The processus descendens divides into two processes (fig. 3), and both calcification and ossification so occur in and over the root of these two processes that when viewed from behind (fig. 4), the appearance given in the model at this stage, viz. 48 mm., is as if there were two separate nodules of cartilage lying in the interval between the two occipital cartilages bounding the incisura posterior of the foramen magnum. The bone which covers the supraoccipital cartilage and tectum occipitale is of a complex nature for it is partly perichondrial and partly dermal (fig. 5). If now figs. 3 and 4 be compared with one another and with fig. 1 which is after Bolk, it can easily be seen how Bolk was led into error. Fig. 3 represents the tectum posterius as viewed from the caval aspect. It will be seen that a bar of cartilage stretches from side to side

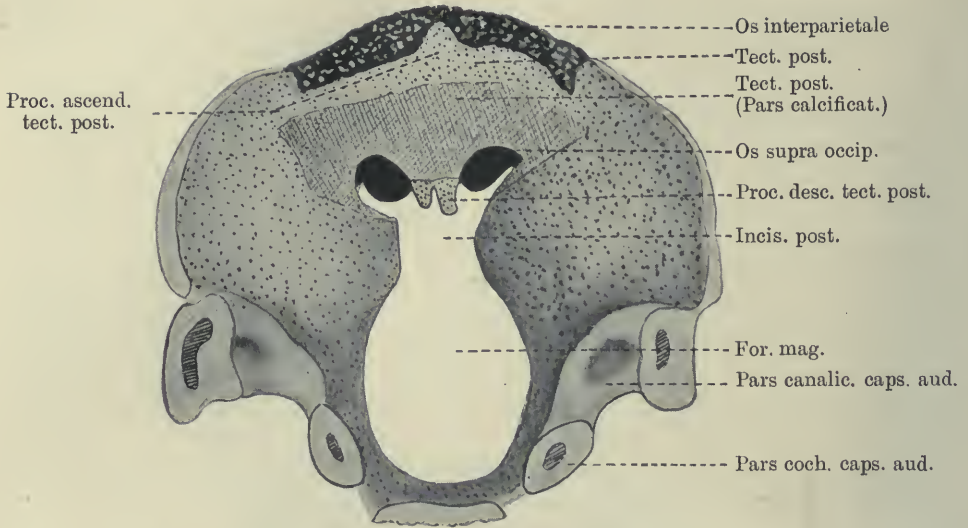


Fig. 3. Hinder part of vault of chondrocranium of human 48 mm. C.R. embryo. Here the tectum posterius appears in its full development giving off in the upward direction the processus ascendens and in the downward direction a processus descendens which divides into two. The stippled parts represent uncalcified cartilage, the cross-hatched part is cartilage in process of calcification.

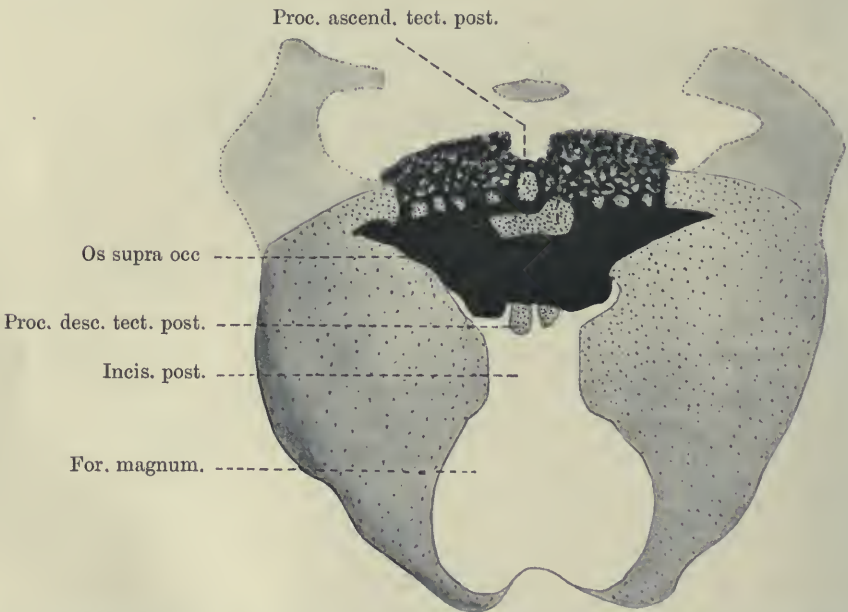


Fig. 4. Reconstruction of the vault of the human chondrocranium at the 48 mm. stage from behind shewing how the processus descendens appears as two isolated cartilages projecting into the incisura posterior and superior of the foramen magnum.

sending upwards a single process, the processus ascendens, and a process which projects downwards and divides into two. It will be seen that a calcified area, shaped not unlike the butterfly area described by Macklin and marked on the figure by cross-hatching, so modifies the appearance of this deep bar of cartilage as to divide it into an upper bar and two lower nodules connected

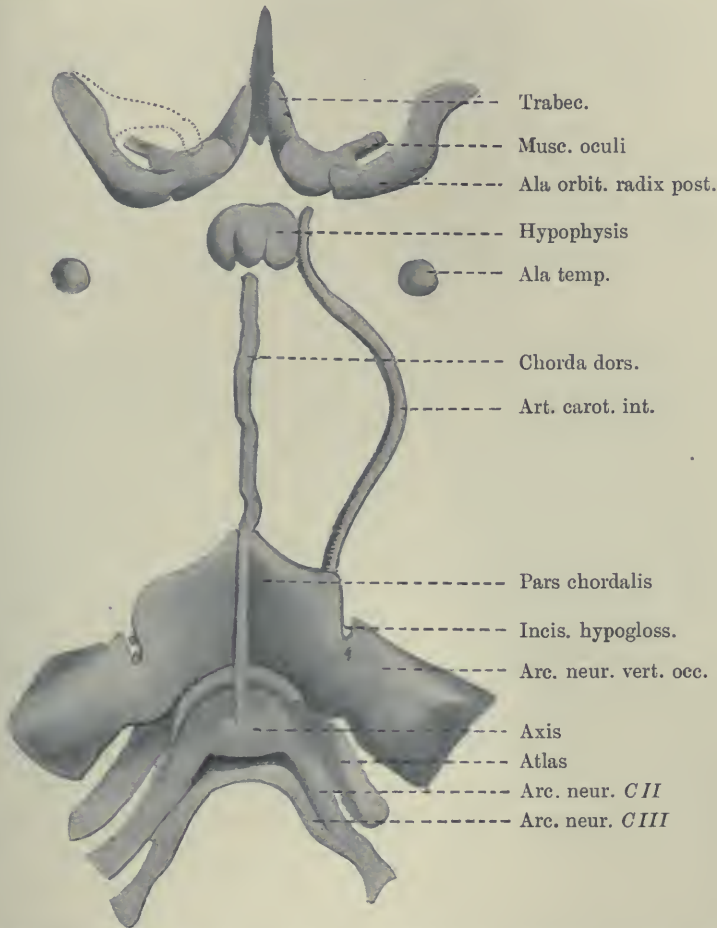


Fig. 5. Model of chondrocranium of 10 mm. *Tatusia* embryo shewing especially the trabeculae diverging behind and giving attachment to the rectus eye muscles; the preoptic limb of the ala orbitalis is not yet laid down. The ala hypochiasmatica is the posterior free extremity of the trabecula of its side.

together above, at their bases, by a narrow band of cartilage. If the same region be now viewed from behind (fig. 4) perichondrial and mixed bone have so extended downwards over the processus descendens as to hide from view even the roots of the two processes and they appear as isolated nodules. Macklin it was who foreshadowed such an appearance, for he says, p. 66, "It is of interest, however, that this upper margin does remain uncalcified and



unossified for such a long period for, as Bolk has shown, it is present throughout his series of four human chondro-crania. In the last, however, it is becoming thinner and more attenuated. I would suggest that this cartilaginous edge may be retained to favour growth of the supraoccipital bone. A similar reason may underlie the persistence of the twin nodules of cartilage which are present in the apex of the superior occipital incisure in Bolk's preparations, and which he states agree in position in one case at least, with the bones of Kerekring. These nodules are apparently (in Macklin's model) in the same position as the processus descendens. It seems to me quite likely that they are not isolated masses of cartilage situated in membrane, but that they are connected with the calcified cartilage of the tectum above."

Fig. 5 shews the central stem of the base of the skull in *Tatusia* at the 10 mm. stage. It consists of a chordal segment and a prehypophyseal part. This latter I have usually termed for topographical reasons the pars interorbito-nasalis. In *Tatusia* this part seems to bifurcate behind and each limb then receives the pre- and post-optic limb of the ala orbitalis from above. The latter being in ontogeny the first to reach the corresponding limb of the pars interorbito-nasalis. That part of each limb of the pars interorbito-nasalis which lies on the floor of the optic foramen is the ala hypochiasmatica and from it the rectus system of eye muscles takes origin. In fig. 5 the muscular origin is shewn, only the post optic limb of the ala orbitalis has joined the pars interorbito-nasalis, but the site of the anterior limb is indicated by a dotted line. There is no lamina hypochiasmatica at this stage. This only appears at the 17 mm. stage when the two limbs of the pars interorbito-nasalis fuse together. The ala hypochiasmatica may thus be looked upon as the edge of the corresponding cornu of the pars interorbito-nasalis which lies below the optic foramen. Should the pars interorbito-nasalis be regarded as the equivalent of the trabeculae, then the alae hypochiasmaticae would be the fore ends of the posterior cornua of the same.

The figures I have submitted prove that Macklin's conjecture is correct and that Bolk's view based on a faulty method is no longer tenable.

My thanks are due to my colleague, Mr D. C. Rayner, for the embryo, and to my assistant, Miss G. R. Llewelyn, for ungrudging help in cutting out wax-plates.

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# A REPORT ON TWO CASES OF HERMAPHRODITISM IN MAN

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## CASE A

THE following description is of a specimen, which was removed from a body in the dissecting room of the Egyptian Government School of Medicine, Cairo, about 15 years ago. No history of the specimen is known. As regards the age, nothing can be said except it was an adult individual.

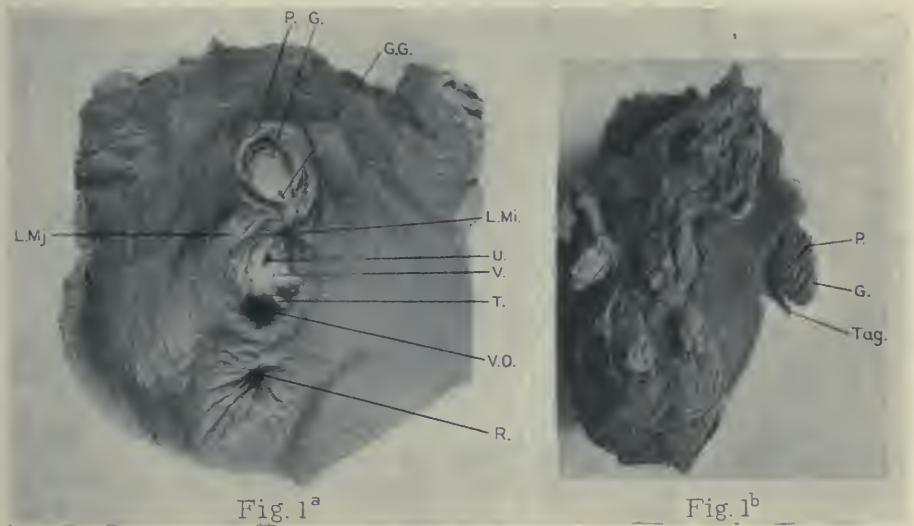


Fig. 1. Anterior and lateral views of external genital organs. *R.* anus, *G.* glans clitoris, *G.G.* genital groove, *L.Mi.* labium minor, *L.Mj.* labium majus, *P.* prepuce, *T.* tag remains of hymen, *Tag.* Tag of skin, *U.* urethral orifice, *V.* vestibule, *V.O.* vaginal orifice.

The specimen consists of female external and internal genital organs. It measures 18 cm. in length, 14 cm. in breadth and 6 cm. in thickness. It has been preserved in formalin solution, and shown in classes as an example of very enlarged clitoris.

*Mons veneris*—is covered with coarse thick hair, which thins out on either labium majus.

*Labia majora*—are shrunk but well marked, and are continuous above with a very large and loose prepuce.

*Clitoris*—is the most striking feature in the specimen. It is very enlarged,

measuring 33 mm. in length with a large glans 16 mm. long and 12 mm. in diameter. It is covered by a prepuce, which is relatively very extensive and can be pulled well over the glans. On its ventral surface there is a groove (*G.G.* fig. 1 *a*) extending to the tip of the glans, having the appearance of the external meatus of the male urethra. The groove is the persistent genital groove of the embryo. There are two tags of skin (*Tag.* fig. 1 *b*) one on either side of the groove at the root of the clitoris. The clitoris as a whole, apart from the large prepuce, resembles the penis of a small boy.

The external orifice of the urethra is 5 mm. in diameter and opens into a well formed vestibule.

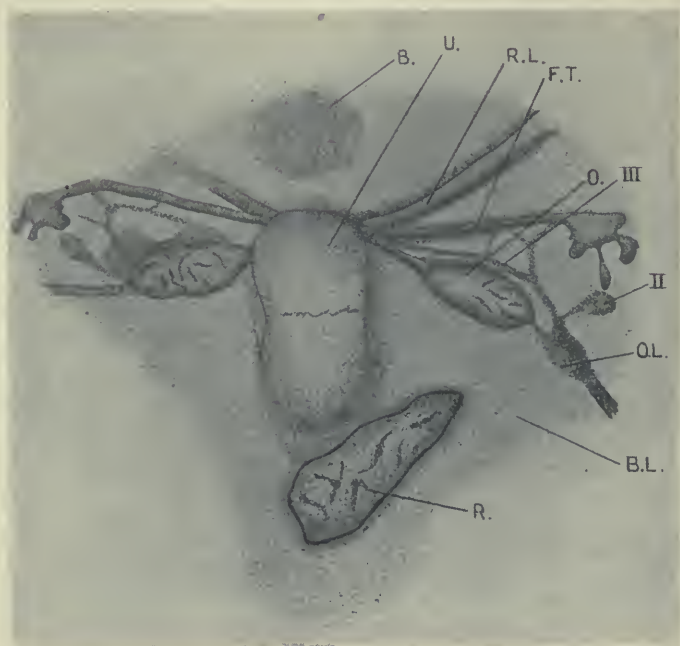


Fig. 2. Internal genital organs. Posterior view. *B.* bladder, *B.L.* broad ligament, *F.T.* Fallopian tube, *O.* ovary, *R.* rectum, *U.* uterus, *II.*, *III.* bands in broad ligament, *R.L.* round ligament.

The vaginal orifice is a large opening, about 20 mm. in diameter and its edge is surrounded by tags, the remains of the hymen. Coitus must have been practised.

*Uterus*—is well formed, normal in shape and size, about 70 mm. long and 34 mm. wide.

*Ovaries*—are well formed, normal in shape and size. Right ovary measures 35 mm. in length, 15 mm. in breadth and 6 mm. in thickness. Its lateral half is puckered, due to rupture of Graafian follicles, and indicates a functioning ovary, but its medial half is smooth. It is connected with the uterus and the pelvic wall by well formed ligaments.



The left ovary is similar to the right, but its puckering is nearly complete and it is situated nearer to the uterus than is the right.

*Fallopian tubes*—are normal in size, shape and position. A section of the right tube was examined microscopically with the result that it was found to be patent.

*Round ligaments*—are normal.

*Broad ligaments*—contain between their two layers bands of thickened tissue. The arrangement of these bands is shown in fig. 2. They can be felt between the thumb and index finger and are seen when the ligament is held against the light. The chief of these bands is a pyriform body (*II*, fig. 2) situated on the lateral side of the ovary. It is about 15 mm. in length, 7 mm. in breadth at its fundus, and about 3 mm. in thickness.

The structure *III*, (fig. 2) lies in a position continuous with that of the canal of Gartner. No dissection of the uterus was made to ascertain the continuity of the canal, but the vestibule was examined for the purpose of finding a possible opening of the canal. No definite opening was found, but this may have been due to the hardness and wrinkled condition of the mucous membrane.

The arrangement of the bands on the left side differs slightly from that on the right as shown in fig. 2.

#### MICROSCOPICAL EXAMINATION

Sections were taken from the right side only at the planes shown in fig. 3.

The opposite side has been left intact to show the arrangement and continuity of the bands.

*Right ovary*—shows well marked cortical and medullary regions (fig. 4).

The cortex consists of compact fibrous tissue. The germinal epithelium has disappeared except that here and there a small piece is seen in a degenerated condition. This is probably due to the poor state of preservation of the specimen.

In the cortex there are structureless masses, some of which are convoluted, surrounded by a fibrous sheath (*G.F.* fig. 5).

The surface at one spot exhibits a depressed scar (*S.* fig. 5).

These masses are corpora lutea and their presence indicates the pre-existence of Graafian follicles.

The medulla is vascular and the blood-vessels have thick walls; but the striking feature of the medulla is the presence of tubules. These tubules are lined by a single layer of cubical cells with large nuclei.

The nuclei stain very badly; some of the slides were left in Delafield's haematoxylin for over 1½ hours without any appreciable effect on the nuclei resulting. The tubules have different shapes; some are circular, others oval,

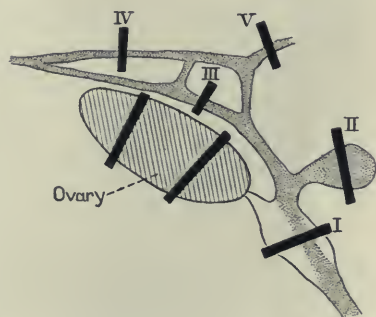


Fig. 3. Drawing of the planes of sections.

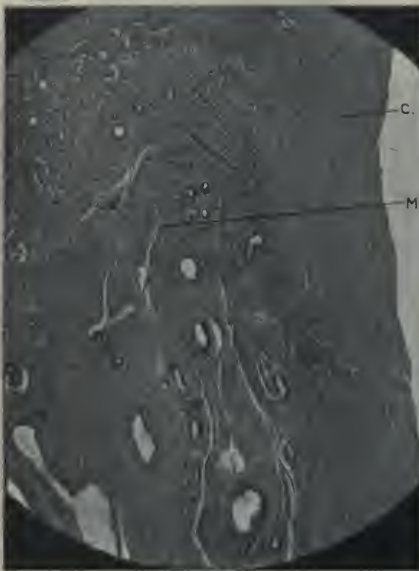


Fig. 4

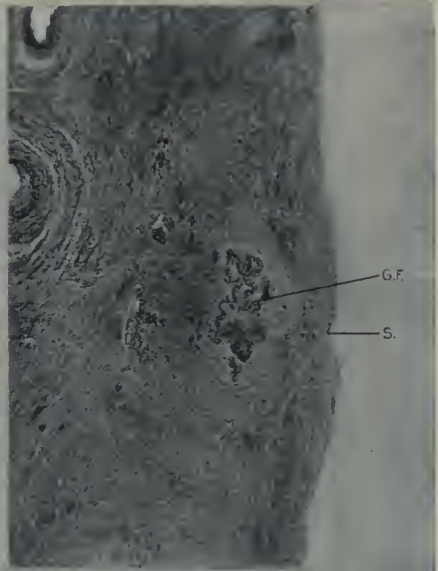


Fig. 5

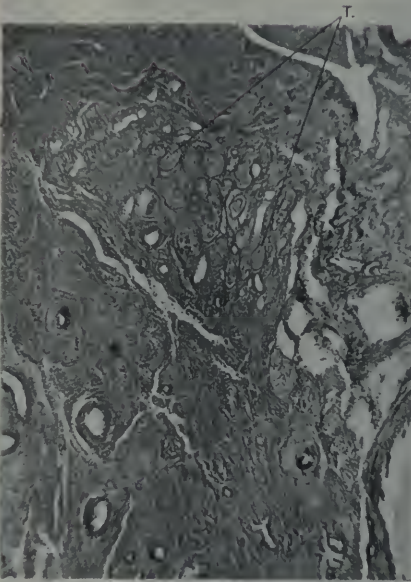


Fig. 6<sup>a</sup>

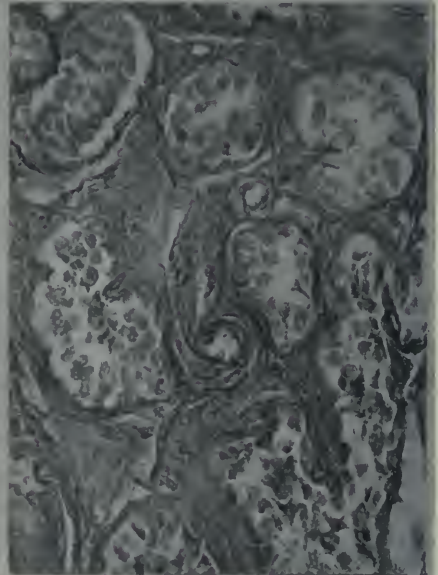


Fig. 6<sup>b</sup>

Fig. 4. Microphotograph of right ovary showing cortex (c.) and medulla (M.).

Fig. 5. Microphotograph of the cortex showing an old ruptured Graafian follicle (G.F.) and a scar (S.) on the surface opposite to it.

Fig. 6. Microphotograph of medulla showing tubules (T.). a, low power, b, high power.

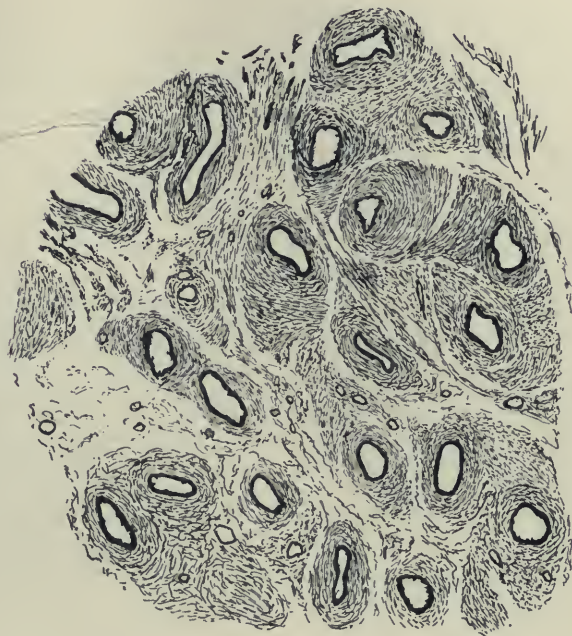


Fig. 7 *a*

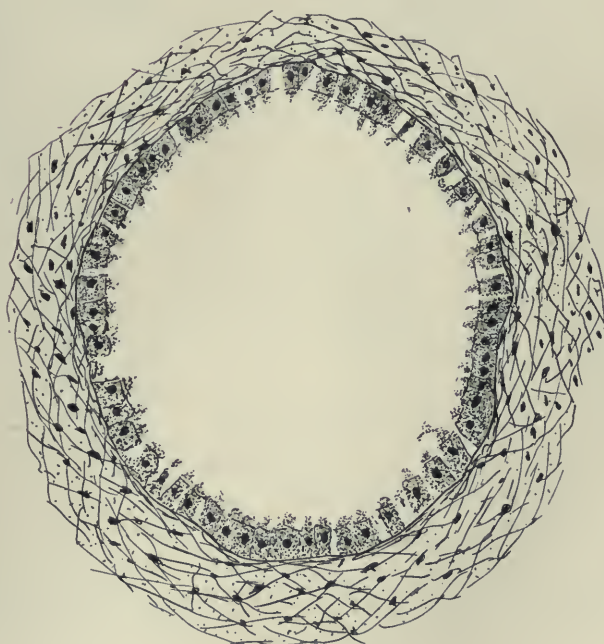


Fig. 7 *b*

Fig. 7. Microphotograph of band *II*. (fig. 3) showing the tubules (*a*) and cilia (*b*)



**S**-shaped or longitudinal according to the plane of section. The tubules in the upper and lower parts of the medulla are more or less circular in section while those occupying an intermediate position are longitudinal. In other words the tubules in the upper and lower parts are disposed in the long axis of the ovary, while the intermediate tubules occupy its short axis. Each tubule is surrounded by a well formed fibrous sheath, from which the cells are detached in some places owing to shrinkage. The tubules are only seen in the medial half of the ovary, which corresponds to that part the surface of which is smooth and not puckered (fig. 2).

The nature of these cells is difficult to determine as cytological examination is impossible. They undoubtedly line tubules, and the question arises, are they testicular cells in an embryonic condition or germ-epithelium cords (Pflüger's tubes) enclosed in the medulla? Pflüger's tubes are, as a rule, solid cords more likely to be found in the cortical region beneath the germinal epithelium, and in them certain large cells are conspicuous. These large cells are the primordial ova. The tubules were not found in the cortex of this ovary in any of the sections examined; but were found abundantly in the medulla. Their lining cells are more or less uniform in size. Near the cortex they lie in the long axis of the ovary, i.e. parallel to the cortex.

#### BANDS IN THE BROAD LIGAMENT.

Sections were taken from the different bands in the broad ligament. The planes of these sections are shown in fig. 3. The most characteristic of these sections is the one marked *II*, in fig. 3 and is shown in fig. 7 *a* and *b*.

This shows tubular tissue surrounded by a well marked fibrous stroma. The tubules are circular, oval or **S**-shaped according to the plane of section. Each tubule is lined by a single layer of columnar cells. The nuclei of the cells are large, basal in position and stain badly. From the free end of the cells protoplasmic processes project into the lumen of the tubules. There appears to be more than one process for each cell, suggesting the presence of cilia. These tubules are remnants of the Wolffian body and they simulate the epididymis in man, which arises from the cephalic part of the Wolffian duct.

#### OTHER SECTIONS.

Band *III*, in fig. 3 is shown in section fig. 8.

This shows a thick walled tubule which represents the rest of the Wolffian duct and from which the vas is formed in man.

Bands *I*, *IV*, *V*, (fig. 3) are shown in sections, figs. 9, 10, 11.

All the sections exhibit tubules and numerous vessels, the vessels having thick walls and large lumina. The significance of the marked vascularity and the great thickness of the vascular walls is not obvious, they may represent an embryonic condition.

CASE B

A patient was admitted to the female wards of Kasr-el-Eini Hospital, Cairo, with the object of having (her) vagina enlarged as (she) wished to get married.



Fig. 8



Fig. 9

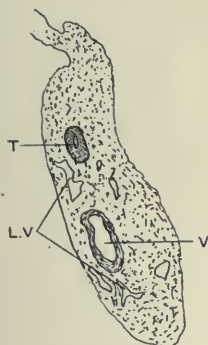


Fig. 10

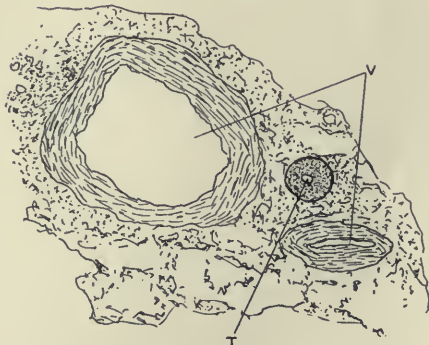


Fig. 11

Fig. 8. Microphotograph of *III.* (fig. 3) showing a tubule (*T.*) resembling the vas in man, and thick walled blood vessels.

Figs. 9, 10 and 11. Microphotographs of bands *I.*, *IV.*, *V.*, showing *T.* tubules, *V.* thick walled blood vessels, *L.V.* lymph vessels.

On examination the gynaecologist reported that the vagina was very narrow and about 3 cm. in length. It ended blindly (atresia vaginalis). No

uterus, tubes or ovaries could be felt. The following measurements were taken:

		Case B	Normal from Eden's text on Midwifery
Interspinous diameter	...	22.0 cm.	25.0 cm.
Intercrural diameter	...	27.5	27.5
External conjugate diameter		16.0	20.0

Age 30 years. Had been brought up and dressed as a girl. Height with bare feet 170 cm. No history of menstruation.

Two years ago (she) went to a doctor owing to "feeling peculiar in the genitals."

The doctor removed two tumours, one from either labium majus. He states in his note that the tumours were two testes with their vasa. He unfortunately threw them away without having them examined microscopically.

The voice, manners, attitude, and features were those of a man. (She) had a slight moustache but no beard. (She) stated that after the removal of the tumours (she) had had sexual desire towards men. Before the operation (she) had no sexual inclination towards either sex. (She) worked in the fields doing a man's work.

When examined in the nude state (fig. 12) the shoulders, pelvis, breast and muscular prominences were found to be typically male as were also the hands and feet. The pubic hair was shaved—an Egyptian custom.

The labia majora were well formed and showed the operation scars (S. Fig. 13).

The clitoris had been removed in childhood—circumcision of the girls being an Egyptian custom among the lower classes. Its root was prominent measuring 15 mm. in diameter, thus denoting a large organ.

The vaginal orifice was very narrow and there was no sign of a hymen. The urethra opened into a vestibule female in type.

The labia minora were slight but well marked.

There was no record of a similar condition in the family.



Fig. 12. Note male shoulders, breast, pelvis, hands.



SUMMARY.

Case A shows the following features:

1. An enlarged clitoris with a ventral groove, an attempt to form a male penis and urethra.
2. The broad ligaments contain well developed remnants of the Wolffian bodies especially in part II. fig. 2. In this part there are tubules with ciliated columnar epithelium, simulating the male epididymis.

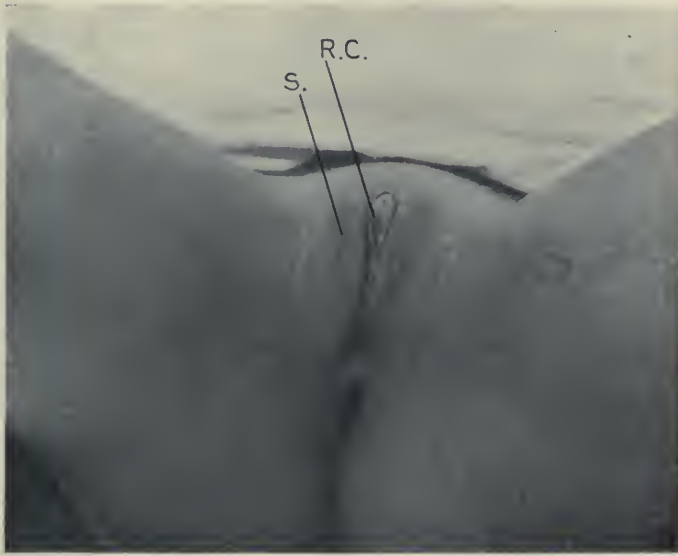


Fig. 13. External genitalia. *R.C.* root of clitoris, *S.* scar of operation.

3. The ovary shows well marked cortical and medullary regions. In the cortex there are remains of Graafian follicles. In the medulla there are tubules lined by a single layer of large cubical cells and, most probably, testicular in nature.

Case B shows the following features:

1. Male characters as far as manners, voice, absence of female breast, shoulders, pelvis and general appearance are concerned.
2. Vagina very small and ending blindly, with no sign of hymen.
3. No uterus, tubes or ovaries could be felt.
4. Presence of two tumours one in either labium majus. These tumours are believed to have been testes.

CONCLUSION

Unfortunately the two cases are incomplete. No history is known of case A and no microscopic examination was made in case B. But I venture to deduce a few points from the above observations.

In case A the external and internal genital organs are, apart from the

enlarged clitoris and the remains of the Wolffian bodies in the broad ligaments, of the normal female type. That she has had functioning ovaries is shown by the presence of Graafian follicles. There is no evidence that she has had children, but there is also no evidence against her having had any. Physiologically she is a female and morphologically she is predominantly female.

Case B represents another type. No female internal genital organs could be felt, i.e. the Mullerian ducts had, as is usually the case in the male, failed to develop. The external genital organs are at first sight of the female type, but close examination shows that the vagina, so-called, is only a small invagination and possibly represents morphologically a uro-genital sinus and is not derived from the Mullerian ducts. The absence of a hymen seems to support this view. The presence of the testes in the labia majora seems to show that the two halves of the scrotum have failed to meet in the middle line, a condition sometimes seen in hypospadias. Therefore case B is morphologically an imperfect male, but functionally (she) is a neutral individual.

What causes the clitoris in case A to enlarge and retain the genital groove thereby simulating a penis? "Embryology teaches that the mammalian embryo is potentially a hermaphrodite and the differentiation into an ovary or a testis is followed by a corresponding development of the correlated sexual organs (2)." It is further believed that the genital glands control the development of the secondary sexual organs, probably by means of internal secretion. It seems that the internal secretion does not only stimulate the development of the correlated secondary sexual organs but inhibits the development of the organs of the opposite sex. This is a point which requires confirmation by further investigations on the internal secretions. The tubules in the medulla of the ovary of case A resemble testicular tubules in an embryonic condition. If they are testicular in nature they will account for the peno-clitoris and the epididymic structure in the broad ligament. They will also support the view that "the embryonic genital gland is composite, the testicle develops within the medullary or central part of the gland, the ovary from its cortical or more superficial parts (1)."

Case A will also show that the presence of physiologically functional genital glands of one sex is not incompatible with the presence of genital tissue of the opposite sex. Cases have been reported by surgeons who have found in the hernial sacs of apparently normal individuals the genital organs of the opposite sex. Brossard (Cairo) operated on a man 26 years old in order to remove a tumour from the scrotum. This tumour proved to be a uterus measuring 9.5 cm. in length, and situated in a sac within the tunica vaginalis. The genital glands associated with it were testes which were normal and in which spermatogenesis was active. Arnolds removed from a man 59 years old, and otherwise normal, a hernial sac containing a bicornuate uterus. Keiffer removed a uterus from a hernial sac of a man, "the father of 8 children (1)." In these cases no microscopical examination of the testes was made. Bland-Sutton reported a case of a boy "who has male external genital organs with un-

deseended testicles." The penis was normal in shape and size. The scrotum was apparently normal but empty of contents. Situated above the prostate was a uterus of the size and shape corresponding to that of a girl of the same age. The genital glands occupied their proper relation to the Fallopian tubes but presented the smooth ovoid contour of a testis. On microscopical examination the glands were found to be testes." It is not stated whether the whole glands were examined microscopically or only a part.

What caused the failure of the external genital organs in case B to develop into normal male organs? Was it due to imperfect testes (pseudo-hermaphrodite) or was it due to the presence of ovarian tissue either in the testes or in the abdomen, a true hermaphrodite? It is not possible to answer this question definitely as the testes were thrown away and the abdomen was not opened. However Gudernatsch reported a case very similar to case B. His case was that of an individual brought up as a female. The external genital organs were of the female type but the clitoris was extremely enlarged. The vagina ended blindly and no uterus was present. The mammary glands were not developed. A tumour was removed from the right inguinal region. The tumour proved to be a testis. In the testis was imbedded a nodule 3 mm. in length 2 mm. in width and thickness which proved to consist of ovarian tissue. The smallness of the ovarian nodule shows how easily it can be missed should only a part of the testis be microscopically examined.

My thanks are due to Professor Derry for his great encouragement and very valuable suggestions and criticism, to Dr Amin Bey for putting the specimen of case A at my disposal, to many other members of the staff of Kasr-el-Eini for their help in many ways and to Mr F. W. King, assistant in the Physiological Laboratory, for helping me in taking the microphotographs.

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## MALFORMED HEART WITH REDUNDANT AND DIS- PLACED TRICUSPID SEGMENTS AND ABNORMAL LOCAL ATTENUATION OF THE RIGHT VENTRICULAR WALL

BY ALEXANDER BLACKHALL-MORISON, M.D., F.R.C.P.

IN 1920 there were published by Dr Shaw and myself in the *Journal of Anatomy* (Vol. LIV, p. 163) particulars of a case under my care in the Great Northern (now Royal Northern) Hospital which showed combined cardiac and genito-urinary anomalies. The cardiac condition consisted in a redundancy of the anterior, low insertion of the posterior, and rudimentary state of the septal cusp of the tricuspid valve. The right ventricle was dilated and hypertrophied, the auriculo-ventricular orifice wider than usual and the clinical signs indicative of the condition were a tricuspid regurgitant bruit and strikingly marked accentuation of the first sound of the heart. The patient died of tuberculous meningitis.

On the 27th of February, 1922, there was brought into the Royal Northern Hospital the dead body of a man, 33 years of age, on whom an inquest was held and in the course of post-mortem examination, Dr Shaw, the Pathologist to the hospital, found a cardiac state which reminded him of the case to which I have already referred, and which we reported together to the Anatomical Society. He saved the heart for my inspection and examination in detail, and has given me permission to exhibit it to the Society on this occasion.

No particulars of previous illness transpired at the inquest and discovering the address of the widow later, I learned from her, to whom I addressed a series of questions, the following particulars which may be given in her own words: "He made no complaint of any kind during the years I knew him. His occupation was that of an electrical condenser maker. No doctor has attended him for the past twelve years. He appeared to be a fully healthy man and only appeared to be extremely tired at times. He appears to have had no knowledge of any defect until rejected when a candidate for the police at the age of twenty-one years." I was also informed from another source that he had been rejected when examined for military service during the war, on account of a cardiac defect which was detected. He therefore evidently gave some physical signs of his condition although not subjectively suffering.

The pathologist's notes of the necropsy are as follows: "*Summary.* Congenital malformation of tricuspid valve. Body of a well-nourished man. No evidence of external injury or violence. Hypostasis present posteriorly. *Head.* No wounds on scalp. Membranes natural, brain 51 ozs. natural. Skull vault and base natural. *Chest.* Pleura; old adhesions between parietal and visceral

layers. Lungs: right, 21 ounces, left, 17 ounces. Both (with) passive hyperaemia.

*Heart and Pericardium.* Weight 15 ounces. Right side much dilated and wall of ventricle very thin. Tricuspid orifice admits (the) whole hand easily. Segments attached very irregularly to wall of ventricle. Septal cusp small and vertical; posterior cusp attached low down; right cusp reaches about to apex. Large area of wall of ventricle situated above the attachments of the segments. Other valves natural. Pericardium natural.

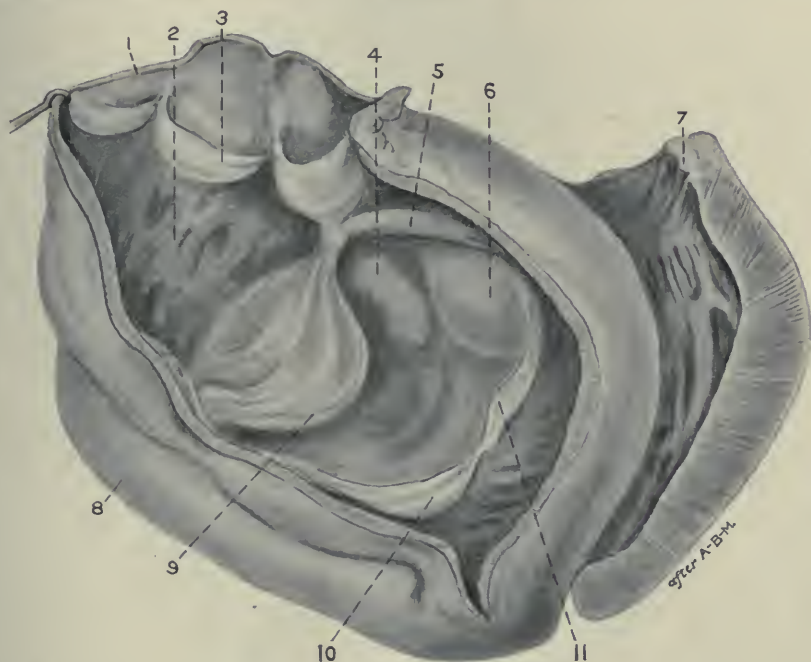


Fig. 1. Malformed heart with attenuated area in right ventricle and low insertion of tricuspid segments, the anterior cusp being redundant. 1, pulmonary artery; 2, conus arteriosus; 3, pulmonary semi-lunar valves; 4, large pars membranacea septi illuminated from the left ventricle; 5, papillary band; 6, internal cusp of tricuspid valve; 7, left ventricle; 8, right ventricle; 9, anterior cusp of tricuspid valve; 10, 11, posterior cusp of tricuspid valve.

*Stomach.* Evidence of recent meal. Passive congestion of mucous membrane. Intestines natural.

*Kidneys.* Weight together  $11\frac{1}{2}$  ounces. Firm. Capsule strips easily. Size natural. Passive hyperaemia. *Liver.* Weight 61 ounces. Passive hyperaemia. *Spleen.* Weight 5 ounces. Size natural. Firm. Slight congestion."

The following are the more exact measurements which I made and the details of the heart in question.

Pulmonary arterial circumference, 8 cm.; valves normal. Tricuspid valvular orifice (for it is not the atrio-ventricular orifice), 7.5 cm. by 7.5 cm.; anterior cusp 4.5 cm. deep, 6 cm. long; posterior cusp 2 cm. in depth at deepest, 5 cm. long; internal cusp 2 cm. deep, 3 cm. long.

Pars membranacea septi 2 cm. by 2.5 cm. Right ventricle 10.5 cm. by 8.5 cm.; ventricular wall 4 to 5 mm. at thickest.

Base of the anterior segment of the tricuspid valve attached at the auriculo-ventricular junction and the segment itself to either side of a large *flattened* papillary muscle from the lower end of which a second papillary muscle gives attachment to the outer end of the posterior segment; the *base* of which is

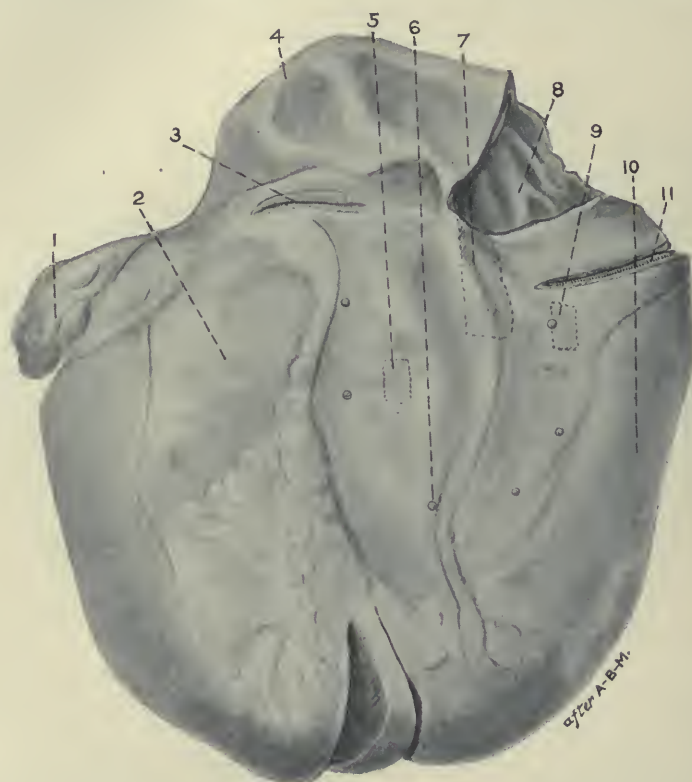


Fig. 2. Malformed heart with attenuated area in right ventricle and low insertion of tricuspid segments, the anterior cusp being redundant. 1, left auricular appendix; 2, left ventricle; 3, coronary sinus laid open; 4, right auricle; 5, 7, 9, portions removed for microscopic examination; 5, in attenuated area of right ventricle; 7, in auriculo-ventricular boundary of attenuated area; 9, in right border of attenuated area; 6, one of a series of pin-heads showing the extent of the attenuated area; 8, muculi pectinati at the entrance to the right-auricular appendix; 10, the left ventricle; 11, the right coronary artery laid bare. B.O. male aet. 33 years.

3.5 cm. from the ventricular apex and 5 cm. below the auriculo-ventricular line. A very much attenuated portion of the posterior ventricular wall in the shape of an inverted triangle, measures 4.5 cm. by 5 cm.

The right auricle measures 7.5 cm. by 5 cm. Its wall is thickest, 1 cm., at the anterior part of the circumference of the superior vena cava and over the rest of the cavity is from 2 to 3 mm. thick. The foramen ovale is closed and large, measuring 2.5 cm. by 2.5 cm.



The coronary sinus is normal in position and has a short Thebesian valve. The inferior vena cava is normal and shows a Eustachian valve. The auricular appendix is likewise normal and the muscoli pectinati well-marked.

The left ventricle measures 8 cm. by 7.5 cm., the average thickness of its walls being 1.5 cm. The aortic and mitral valves are normal. The right coronary arterial orifice is large, the left small. There is some atheroma in the sinuses of Valsalva. The aortic circumference is 6 cm.

The left auricle measures 10 cm. by 4.5 cm. Its walls average 2 to 3 mm. in thickness. Microscopic sections of the attenuated area, at the level of the coronary vessels (sulcus), and far above the insertion of the posterior segment of the tricuspid valve show the auricular to be quite distinct from the ventricular musculature and demonstrate the area in question to be purely ventricular. Sections from the most attenuated part of this area show a sheet of muscle, while its lateral junction with the thicker ventricular wall is in normal muscular continuity. Any muscular action of this area would follow auricular systole, but tend to open, not to close, the tricuspid valve.

The subvalvular portion of the ventricular cavity is thus limited abnormally, and, notwithstanding the capaciousness of the anterior segment of the tricuspid valve there must have been free regurgitation and all round blood pressure in the chamber which accounts for the abnormal size of the valvular orifice and the general thinness and flattening of structures in it. The weight of the heart being fifteen ounces, that is, rather over the average weight of the normal male heart, shows that some attempt at compensatory hypertrophy had been made to deal with the circulatory difficulty. A noteworthy fact is the relative position of the internal cusp of the tricuspid as regards the pars membranacea septi and as regards the papillary band, which is the left attachment of the anterior segment; the pars membranacea being posterior to and not covered by the internal or septal segment, a fact which may have developmental significance. Like the membrane closing the foramen ovale, the pars membranacea is abnormally large, but both the auricular and ventricular septa are complete, while the chief papillary muscle is quite flattened. The coronary sinus is normal in position, and the auriculo-ventricular bundle of His may be, but the latter point has not been determined positively. Sections of a large branch of the right coronary artery in the right auricle show considerable thickening of the intima and some flattening of the lumen, but there is no general increase of intima in the arteries, taking the membrane of Henle as a guide. There is neither naked-eye nor microscopic evidence of muscular deformation and sections of a papillary muscle from the left ventricle show no interstitial increase, but sections from the attenuated area in the right ventricle reveal a loose spreading intercellular connective tissue. The attenuated area is not degenerative and pathological, but developmentally deficient.

The break in the continuity of the fibrous ring at the auriculo-ventricular boundary of the area of attenuated ventricular wall which allowed distension, together with the low position and ineffective closure of the valve segments

resulting in the dilated dextral chambers, is a striking testimony to the importance of the fibrous support of the valvular apparatus and of the valves themselves, in the cardiac mechanism of the circulation. It was the fashion not long ago to decry the importance of the integrity of this factor. One rarely meets with such eloquent evidence to the contrary as is afforded by this case and the importance of this factor is not less but greater in the left or systemic arterial heart.

In the unfortunate absence of a record of the clinical signs in the case of B.O. some of the clinical physiology must be left obscure, but much may be deduced from the anatomical details given. His sudden death without a history of previous ill-health is interesting, as in many other cases of heart disease so dying. I shall not, however, comment further on this fact, beyond stating my belief that, if in the case of B.O., the foramen ovale had remained patent, it is probable that he would have lived longer. In support of this opinion, I may recall to the memory of members of this Society the case of an old man of whom I gave an account in 1917 (Vol. LII, p. 251), and who, with an almost obliterated pulmonary artery and very hypoplastic or rudimentary right ventricle, lived to a venerable age, because he had, like B.O., a sound left heart, but also a widely patent foramen ovale, which gave easy access of the right heart blood into the left chambers.

## FAMILIAL ABNORMALITIES OF THE MIDDLE PHALANGES OF EACH HAND

BY R. C. D'ARCY HANN, B.A. (CANTAB.)

THE condition about to be described seems extremely rare, a search of what literature is available revealing no parallel case.

It is to be regretted that a more detailed account cannot be given owing to difficulties made by the patient: for example, an examination of the feet was refused and of the family history it was only certain that of seven or eight members similarly deformed the mother, her brother, and sister were included. The man examined had no brothers and only one sister and she was unaffected.



The mother and son were seen and the condition on examination seemed exactly similar. The radiograph and description is that of the son aged 19. The hands were not greatly ill-shaped though they had an appearance of squatness; the first impression on inspection being that all the first interphalangeal joints were missing. The movement at the terminal joint was very



free and so comparatively little disability of the hand resulted. On examination of the radiograph the striking feature is the restriction of the abnormality to the second phalanges, all of which are involved.

The deformity is symmetrical but for the fact that in the ring finger of the left hand the segment representing the second phalanx has become united to the proximal phalanx. The bone representing the second phalanx varies from a small fragment in each little finger (strangely displaced laterally) to well formed segments, with normal joints above and below in the ring and index fingers, whilst in the middle finger and right ring finger the segments have actually fused. The line of union is obvious and there has been no suggestion of a joint.

We may also note a tendency to a displacement of the terminal phalanges towards the middle line of the hand.

There seems no doubt that the proximal and terminal phalanges are normal and the interpolated bones are not abnormal epiphyses.

An interesting comparable case was published by Dr Drinkwater (in this journal)<sup>1</sup> of a family showing abnormal segmentation of the index and middle fingers. The fault there was entirely confined to fingers whereas here only one phalanx is concerned.

Under the belief that a hand deformity existed throughout many generations of an old family of the British Peerage the writer, in answer to a letter he had sent, received an account from a well-known member of the family.

She writes: "Some of my great uncles had deformed joints in their fingers, the first joint being absent, and two of them had only one joint in each thumb. My own aunts and uncles all had perfect joints, but I personally have only one joint in each thumb."

The writer is indebted to Dr Scargill for the excellent radiograph.

<sup>1</sup> *Journ. Anat. and Phys.* vol. L. 1916.

# A CASE OF ARRESTED DEVELOPMENT OF THE THYROID GLAND ASSOCIATED WITH DWARFISM AND GREAT OBESITY

By CECIL McL. WEST, M.C., M.B.

*University Anatomist, Trinity College, Dublin*

THE unusual condition in the thyroid gland, and other anatomical peculiarities in the present case make it, I think, worth recording.

The case was that of a female subject well advanced in years (the exact age is not known), which came into the Anatomical Department of Trinity College, Dublin, some months ago. The subject was an obvious dwarf, being only 4 feet 4 inches in height. The subject suffered from marked obesity, there being four inches of fat in the lumbar region just above the iliac crest, and in other regions the fatty layer was correspondingly thick.

The skin was thrown into numerous folds round the limbs; the face was large and fat, the nose was squat and splayed out on the face, the root being much retracted. The lips were thick and coarse, the whole face had a distinctly myxoedematous appearance. Hair was plentiful on the head and there was a considerable growth on the upper lip.

The limbs were short and fat, and the hands had somewhat the appearance of the "main en trident."

The muscles were well developed with short thick bellies. Especially well developed were the subcutaneous muscles, such as the occipito-frontalis.

There was considerable increase in the fibrous tissue, which was very noticeable at the points of attachment of the muscles to bone, as for instance was the case in the trapezius and in the pectoralis major.

The capsules of the shoulder and hip joints were much stronger and thicker than usual.

The vessels were somewhat larger and more tortuous than usual. The common carotid artery divided at the level of the hyoid bone. The heart was very fatty, but otherwise appeared normal.

The nerves were larger and thicker than usual, and some of the larger nerves, such as the sciatic and the branches of the brachial plexus ran a tortuous course, suggesting that they were too long in comparison with the neighbouring structures.

The base of the skull was considerably reduced in the antero-posterior diameter, the length from basion to nasion being 84 mm., as against 95 mm. which I found to be the average length in 27 normal skulls. This explains the retraction of the root of the nose, already noted, and in this respect the

condition of the skull is like that seen in achondroplasia, but there the resemblance ends. The characteristic flattening of the base of the skull and the great expansion of the cranial vault so often seen in achondroplasia were absent. The bones of the skull were rather thicker than usual.

The long bones of both extremities were very short; the arrest in development affecting the shafts rather than the epiphyses, which seemed too long for the shafts.

Muscular markings were very well shown; this feature may have been associated with the increased quantity of fibrous tissue, already noticed in the muscular insertions.



Fig. 1. Camera lucida drawing of face and neck from left side. A. Thyroid gland. B. Parotid gland. C. Sublingual gland. D. Submaxillary gland. E. Anterior belly of digastric.

In both the shoulder and hip joints there was evidence of arthritis deformans; the head of the femur was much flattened and a new pressure articular facet had been formed on the summit of the great trochanter. The tibia and fibula were of almost the same length, and the greater length of the fibula over the tibia often seen in achondroplasia was not observable. The relative lengths of the long bones to each other was normal, the upper and lower limbs being affected to an equal degree. The pelvis was narrowed, especially in the antero-posterior diameter, the conjugate measuring 84 mm. and the transverse diameter 122 mm.

On opening the abdomen the great omentum and mesentery were found to be loaded with fat; the liver presented a curious appearance seeming at first sight to be transposed, but this was found not really to be the case, but the



left lobe was like the normal right lobe in appearance and the right lobe was like the normal left lobe; the relationship of the various neighbouring structures was as is seen in the normal subject, the inferior vena cava being placed to the right of the Spigelian lobe, and the stomach occupying a concavity on the inferior surface of the large left lobe.

The internal genitalia appeared well developed and were very easily seen owing to the contracted state of the pelvis.

There was no evidence of the thyroid gland in its usual position but in the middle line just under the mandible, a tumour was found, having the shape and size of a golf ball. This was not noticed at first owing to the great accumulation of fat in the neck region.

The tumour was slightly moveable in the vertical and horizontal planes, and was fixed to the anterior surface of the hyoid bone by a short pedicle. On examination this tumour was found to be the thyroid gland.

The gland had on its superficial surface a rich venous plexus, and was covered with a thin film of muscular fibres derived from the anterior bellies of the two digastric muscles which were spread out over it.

The mylohyoid muscles did not meet in the middle line but were separated from one another by the thyroid gland, and in addition the left sublingual gland, which was apparently much enlarged had sunk down in front of the anterior border of the left mylohyoid muscle and was lying in the digastric triangle. The geniohyoid muscles of each side were spread out over the thyroid gland, the right muscle passing down to the hyoid bone and the left one

being inserted into a capsule which enclosed the gland. As has been mentioned the gland was attached to the anterior surface of the hyoid bone by a short pedicle. The dissection was carried laterally to determine the blood supply of the gland, and it was then found that all the salivary glands appeared to be much increased in size. On microscopical examination it was found that the apparent increase in size was due to the great accumulation of fat among the lobules of the glands and not to any actual increase in the size or number of the glandular cells.

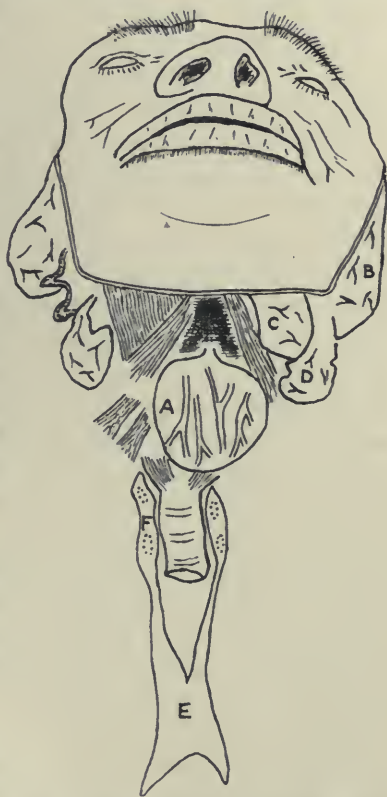


Fig. 2. Semidiagrammatic camera lucida drawing of face and neck from in front. A. Thyroid gland. B. Parotid gland. C. Sublingual gland. D. Submaxillary gland. E. Mass of fat extending into the thorax and containing thymus tissue. F. Mass of fat lying on each side of the trachea and having embedded in it parathyroids (shown by dotted lines).

The thyroid gland received its blood supply almost entirely from the left lingual artery which divided into two branches, one for each side of the gland. The superior thyroid artery also sent a small branch to the gland, but this artery was not nearly as large as usual, its largest branch being that to the sterno-mastoid muscle.

The rich venous plexus which covered the thyroid gland was connected above with a number of veins coming down from the floor of the mouth, and on each side with a number of large veins which ran with the hypoglossal nerve on the hyoglossus muscle. The plexus on the thyroid gland was drained by a large vein which joined the internal jugular.

The tongue was examined but there was no evidence of a foramen caecum or of a thyro-lingual duct.

A portion of the thyroid gland was removed for microscopical examination. On section the superficial part was tough and fibrous, and in the deepest part were quite definite vesicles filled with a colloid-looking material.

The gland was seen to be enclosed in a fibrous capsule; in the superficial part were very small vesicles with hardly any lumen and containing no colloid, and having large numbers of blood vessels lying in close relationship to them. The great vascularity was one of the most striking features of the section. More deeply there was a complete absence of vesicles, and only degenerating fibrous tissue containing small calcareous masses could be seen. More deeply still this fibrous tissue gave place to large distended vesicles filled with colloid. In some places the cells forming the walls of these vesicles appeared flattened out, whereas in others they had undergone proliferation and projected into the cavities of the vesicles, some of the cells here and there appeared to be lying free in the vesicles.

Doctor A. C. O'Sullivan kindly examined the sections for me and believed they resembled those from cases of parenchymatous goitre.

In the position usually occupied by the lateral lobes of the thyroid gland, were two masses of fat lying one on each side of the trachea and passing backwards under the common carotid artery to the sides of the oesophagus.

On turning these fatty masses forwards, two small dark nodules were found embedded in their posterior aspects on each side, one about half-an-inch above the other. On section these proved to be parathyroids. The masses of fat on each side received a blood supply from the inferior thyroid artery which was much smaller than usual. Two veins of quite large size passed from each of these fatty masses, one upwards to the internal jugular vein, the other downwards to the left innominate vein.

The masses of fat were continuous below with a large median mass which extended down into the thorax in front of the great vessels; on section this mass of fat was found to contain thymic tissue.

Portions of the salivary glands were examined microscopically. They contained large quantities of fat which, separating the individual lobules, accounted for the apparent great increase in size of the glands.

The pituitary did not appear to be enlarged. Sections showed a good deal of colloid material in the anterior lobe, great vascularity and the presence of an equal number of eosinophil and basophil cells. The pars intermedia was not at all definite but there was a large quantity of colloid between the anterior and posterior lobes. The posterior lobe appeared normal. The suprarenals did not show any unusual features.

It is now generally recognised, I believe, that the thyroid gland is developed from a single median rudiment which grows down from just behind the tuberculum impar, and that there are no lateral pharyngeal diverticula taking part in its formation. This view is supported by the condition present in the case described. There was no evidence of thyroid tissue in the position usually occupied by the lateral lobes.

That the thyroid mass was attached to the anterior surface of the hyoid bone is what one would expect to find, remembering its mode of development. The parathyroid glands were normally developed.

The mass of fat which occupied the normal position of the thyroid gland coming into close relationship with the parathyroids on each side and being continuous with the median mass in front of the great vessels at the root of the neck and upper part of the thorax is of interest, as it filled very accurately the position occupied by the embryonic thymus gland. As has been noted microscopical sections proved the existence of thymus tissue in this mass.

As concerns the conditions found in other parts of the subject, it was at first thought the case resembled achondroplasia, and in some respects it certainly recalls the condition. The appearance of the face, the retracted nose, the shortness of the base of the skull all bear some resemblance to achondroplasia. The pelvis, although narrow, is however by no means so small as in typical cases of achondroplasia. On the whole, I believe the case most closely resembles myxoedema. There is evidence of deficient functioning of the thyroid gland with an apparent attempt at compensatory hypertrophy in the deeper parts of the organ, and many of the features of the case recall the picture described by R. McCarrison<sup>1</sup> in his book on the thyroid gland, under the heading of myxoedema.

In conclusion I should like to thank Prof. A. Francis Dixon for the help I have received from him.

<sup>1</sup> R. McCarrison, *The Thyroid Gland*, London, 1917.



# AGE CHANGES IN THE PUBIC SYMPHYSIS. VII. THE ANTHROPOID STRAIN IN HUMAN PUBIC SYMPHYSES OF THE THIRD DECADE

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## Introduction

THE Hamann Museum of Comparative Anthropology and Anatomy of Western Reserve University is unique of its kind. Recognised two years ago by formal vote of the trustees, this integral part of the Anatomical Department grew out of the personal collections of Dr Hamann himself as Professor of Anatomy, collections which were intended to illustrate upon the Hunterian principle the life-history of Man and other animals and the diseases to which Man is subject. For years past the trustees have annually subscribed funds to extend and to care for the collections which Dr Hamann originally made and which he has continued so generously to increase. Other gentlemen, notably Dr Weber, Mr Newton T. Baker and Mr G. G. Marshall have associated themselves with this effort and now the Museum is the central feature of the department around and in which the teaching and research of the laboratory are carried on. The unique character of the institution lies not in its size or in its scope, considerable as these are, but in the opportunities which it affords for anatomical work of the most exact type. Dr Hamann had a very large share in formulating the Anatomical Laws of the State and built up a public confidence in the Anatomical Department whereby Municipality and Medical School could share

a common responsibility. This rendered possible the large and growing collection of human skeletons, now numbering 900, with accurate data obtained during the life of the individual. Dr Hamann saw the impossibility of carrying on efficient work without a comprehensive library housed in the Museum itself and provided that most valuable instrument in the first instance, thus saving the staff loss of time which would otherwise have been entailed through having to refer to a general university or centralised library for journal files and monographs while actively engaged in research. Technical help was provided on the same generous scale as the equipment, and the trustees, entering sympathetically into the realisation of this vision, have built up a laboratory which is an inspiration to those who have the privilege of working therein.

On former occasions I have discussed the possibilities for the advancement of anatomy afforded by this organisation and therefore I will content myself now with the simple statement that the object of the researches at present under way is the study of the life-history of Man's body as exemplified by the races on the North American continent, notably of White and Negro stock.

It is with this in mind that during the past ten years we have been examining skeletons of known age, seeking to elucidate the changes in feature, texture and composition of the bones following age, sex and race. Much has been done but relatively little published owing to the necessity of gathering enough data and material to give our statements the authority of proof rather than the suspicion of assertion. It is not the spade work that one has now to consider so much as the presentation of facts. For the investigations have disclosed numbers of untouched problems which can be solved only upon just such a material as we now have here.

In making a survey of the pelvis some three years ago I found that the symphyseal area could yield much information which, though actually of a phyletic nature, might nevertheless be used to help in that most fascinating and elusive of determinations, namely the approximate age or relative position in the life span of an individual of adult and not yet senile years. Just as there is a definite march of the individual through the successive life periods from birth, in growth of youth and metamorphosis of adult life to senility and ultimately to death, so we may recognise the progress in similar stages of various of his tissues. For some of these, the hair and skin and arteries, we realise already the successive phases but in this respect the skeleton has hitherto seemed a document in so strange a language that merely a scattered paragraph or a page at random has been deciphered. Even facts known to occasional writers of the past have sunk into oblivion because they have never found their way into textbooks and but rarely into the current literature of the day.

One finds, however, that, like the other tissues, the skeleton has its age features. They are of a nature peculiar to the tissue of which the skeleton is composed. They do not disclose themselves to the worker in miscellaneous grave-yard material but may be readily ascertained from a large collection of material of known origin, with accurate data, and prepared by a uniform and

standardised method. It has also been possible to show that the changes undergone by bones are not limited to the human skeleton but may be discovered with equal readiness in the skeletons of other animals and, relatively to the life span at least in the case of mammals, at approximately the same periods.

In previous works I have sketched the derivation of the symphysial area from its condition in the Reptilia, its life-history in the Mammalia, its general Eutherian characters and its various phases in Man. For a full discussion of these problems the reader is referred to the following writings:

- I. "The male White pubis." *Journ. Phys. Anthropol.* 1920, III. 285-334.
- II. "The pubis of the male Negro-White hybrid." *Ibid.* 1921. IV. 1-25.
- III. "The pubis of the female White series." *Ibid.* 1921. IV. 26-39.
- IV. "The pubis of the female Negro-White hybrid and assembled results for Man." *Ibid.* 1921. IV. 40-70.
- V. "Mammalian pubic metamorphosis." *Ibid.* IV. 333-406.
- VI. "The interpretation of variations in the symphysial area." *Ibid.* IV. 407-424.

It is one thing to discuss in the light of a large amount of material the general changes undergone by a particular area during the total life period; it is quite another matter to take up a single case and attempt to read from it the indications of age when one has never had the opportunity of consulting the entire material upon which the general statements have been based. This latter procedure is especially difficult in the case of Man whose symphysis has undergone very marked and peculiar specialisation consequent upon the failure of the two pubic bones ultimately to unite in the midventral line. In many cases the writer himself would be puzzled to give an unqualified determination of age unless the rest of the skeleton were at hand to confirm his interpretation and yet there are such possibilities for increasing the research value of a skeleton provided its approximate age can be discerned that it appears worth while to attempt to elucidate in detail the features presented by the human symphysis in order that age determination may be made with greater assurance. Of course I do not mean to lay inordinate value upon the symphysis as an age indicator. It is intended that eventually this portion of the skeleton shall take its appropriate place among the many skeletal age indicators which we have been able to recognise in working over the Reserve material. The field of investigation is so new and the features of skeletal metamorphosis so unfamiliar that essaying age determination upon a single skeleton or a single pelvis may prove an exceedingly discouraging task unless there be at hand a full presentation of the facts upon which the determination may be made. It is therefore my intention in the present paper to discuss the steps by which the well recognised oval outline of the symphysial face becomes built up, the age relationship of these successive phases and the modifications by which these age indications may be obscured.

In order to carry out this intention it is first necessary to give a brief résumé of the general mammalian characters of the area, and also of the features peculiar to Man.



*Mammalian features of the symphysis pubis*

In the reptilian pelvis as represented by *Sphenodon*, the pubis and ischium do not form a continuous symphysis but are separated from each other by an antero-posterior series of elements, namely the epipubis, the median ligament and the hypo-ischium. I have stated my opinion, based upon the work of Mehnert, that the single character of these elements is a secondary condition, and the elements are originally of a bilateral nature. The Monotreme pelvis is essentially reptilian in character and helps us very little. As in the reptiles pubis and ischium take about equal parts in forming the symphysis. The Marsupial pelvis is very different. There is vastly greater difference between the symphyseal areas of the Marsupial and of the Monotreme than between those of the Marsupial and of the Placental mammal. The Marsupial symphysis may well be our starting point.

Fig. 1 shows the symphyseal area of *Petaurus breviceps*, B 187, much enlarged. What I have called the median bar is clearly seen in this example. It expands above into the upper nodule and below into the triangular lower nodule through which it is continuous with the ischial epiphysis on each side. The median bar, the upper and lower nodules are homologues of the median ligament, the epipubis and the hypo-ischium respectively. This median bar extends for a certain distance between the symphyseal faces as shown in fig. 3, *Dendrolagus inustus*, B 193. It is not always visible on the surface. Fig. 2, the upper symphyseal area of *Macropus bennettii*, B 181, shows only the upper nodule from which a slender rod passes deeply down between the symphyseal faces and represents the median bar. Evidently the upper and lower nodules are originally bilateral, the median bar imperfectly so. In fig. 4, *Phascalomys tasmaniensis*, B 601, the beginning of the lower nodule is well shown and it is obviously the continuation of the ischial epiphysis. At a later period in this animal the upper nodule and then the median bar would have developed, the elements of the two sides rapidly uniting. In adult life these elements all fuse with the pelvic halves binding them immovably together. The last traces of the several elements are in process of being lost in fig. 5, a young adult *Odocoileus virginianus*, B 633. In the Virginia Deer in fact the upper nodule rarely exists at all. One of the features which differentiates the symphysis of the Marsupial from that of the Monotreme most strikingly is the very small part taken by the ischium in its formation. There are differences in this respect among the several Eutherian orders but, with one notable exception, all Eutherian orders conform in a general way with the type of symphyseal area found in a typical Marsupial like *Petaurus*. The exception which I desire to emphasise refers not to examples among the Rodents, Insectivores, Edentates, Cetacea, Sirenia and Pinnipedia which have vestigial or highly specialised symphyses, but to the Primates. This order shows still further reduction and finally entire elimination of the ischium from participation in the symphysis with a consequent reduction and loss of the lower nodule as a separate entity.

It becomes merged again into the linear epiphysis extending along the pubic arch. The symphyses of the great Anthropoids form a special link between human and other Primate symphyses for whereas in some the two halves of the pelvis finally fuse at the symphysis, in others this fails to occur and a typical human form of ununited symphysis results. In those specimens in which union takes place a median bar and an upper nodule are formed but no lower nodule appears. The condition is exemplified in Gorilla B 624 (fig. 6). This is really the key specimen to a proper understanding of the human form of symphysis.

Now I have affirmed the bilateral nature of all the three median symphyseal elements, evidence for which is presented elsewhere (v). Upon the basis of this assumption one would expect to find bilateral vestiges of the three structures. These do occur in the human symphysis and are responsible for the upper extremity, the ventral rampart and for the lower extremity, which together complete the oval outline of the symphyseal face. The dorsal margin is not epiphysal in nature but is formed directly from the pubis itself.

In my former work I discussed first of all the features of the human symphysis and later sought to explain the occurrence of its peculiar features by reference to comparative anatomy. In my general survey of the human symphysis I came across many curious divergences from the normal or rather from the modal type—divergences in point of structure and time relationship—which I was quite unable to explain at the moment. It became clear in my last contribution (vi) that many of these anomalies are unquestionably evidence of the relationship of the non-uniting human symphysis to the typical mammalian form through a type such as that figured in the Gorilla (fig. 6). With this assurance it is now possible to trace the development of the human type of symphysis and to group the individual specimens according as they approach or recede from the more characteristic mammalian (or Primate) conformation.

In this communication I propose therefore to present the facts from this new angle and to confirm or correct the statements which I have previously advanced from a study of the human symphysis alone.

#### *Peculiarities of the human symphysis*

In this brief summary of the mammalian symphysis we have seen that there are two distinct elements in the formation of the symphyseal face. The dorsal margin and part of the adjoining surface (dorsal platform) are formed from the pubic bone itself. The upper extremity and ventral margin (rampart) are epiphysal in character. The surface adjacent to the ventral margin is formed, like the margin itself, from the epiphysal element which, as the median bar or disc, penetrates backward between the two symphyseal faces. The lower extremity, like the upper nodule and the ventral rampart, is typically formed from the epiphysal series in continuity with the epiphysis of the ischial tuber. In the Primates, however, this lower nodule is lost early and the majority

of Primates therefore do not show it. The Gorilla symphysis (fig. 6) is a good illustration of this condition. In the event, which in higher Primates is most probable, of the epiphysial series being weakly defined, the lower extremity is not formed by a nodule but fashioned in an ill-defined manner from the pubic bone itself. It is essential to keep clearly in mind the derivation of the higher Primate symphysial face. The dorsal margin and platform and sometimes the lower extremity are formed directly from the pubis; the upper extremity and ventral margin and sometimes the lower extremity are derived from an extension of the epiphysial tongue coursing along the pubic arch from the tuber ischii.

The condition of pubic development in the White stock is so aberrant and retrogressive that it is with difficulty that one can discern the typically Primate features. I propose therefore to take up first of all the appearance of the symphysis in the Negro in which the Primate character is more plainly seen.

Since the description of the male Negro symphysis was written (in the spring of 1921) there have been many accessions to our skeletal collection and fortunately the new specimens fill the gaps formerly existing and clear up many debateable points. It was with some difficulty and hesitation that I originally defined the successive phases of Negro symphysial metamorphosis. Whereas the male White skeletons fell fairly well into line with the scheme finally adopted (I), the male Negroes were at first exceedingly troublesome. The main difficulty was in the order of formation of the extremities and of the ventral rampart. In the case of the male Whites I had been compelled to admit the irregularity in occurrence of the upper extremity (I, p. 307) together with the variability in distinctness of the lower extremity and in the manner of formation of the ventral rampart (I, p. 308). Nevertheless, leaving out of account the exact manner in which these several parts are developed, there is a succession in point of time for the definition of the symphysial outline and this succession may be usefully employed as an age indicator. The appearance of the Negro symphysis is much more difficult to evaluate, not because it is erratic, but because the whole description of symphysial metamorphosis was based in the first place upon the White stock. The Negro partakes to a somewhat greater extent of and certainly shows more plainly the more typical Primate features and it is these very Primate modifications of the modal mammalian symphysis which introduce a confusing element. While the Negro features were read in the light of those exhibited by the White stock and have been so described it became evident that much greater progress would be made in the interpretation of the Negro features if a survey of the mammalian orders were undertaken first of all. We now find ourselves with that information to hand and particularly with the very suggestive knowledge that among the giant Anthropoids there are two distinct types of symphysis, one in which fusion takes place about phase VII, whereas in the other the symphysis remains unfused throughout life exactly as in the human condition.

Now this differentiation of the Anthropoid symphysial metamorphosis into



two types, one partaking of the general mammalian character, the other clearly forming a link with the appearance of the human symphysis, indicates that we may be justified in looking for different types in the human symphysis itself and these have already been discussed in a very general manner. In my study of variations of the area I have mentioned that "as for any Stock-linked character in variations the evidence is not as yet very strong but there does seem to be some indication that the Negro-hybrid symphysis is apt to partake of a more typically Primate character" (vi, p. 422). It was necessary to wait for more material before making a categorical statement upon the subject and our greatest need was for material in the third decade of life. This addition of material has now been obtained and by its help we are enabled to derive a convincing demonstration of the essential truth of this statement.

*An anthropoid strain in the Negro symphysis*

In the immediate post-adolescent stage there is no obvious difference at the symphysis pubis distinguishing the Negro from the White. Phase I has been defined as having the following distinguishing characters. Symphysial surface rugged and traversed by horizontal ridges separated by well-marked grooves, the ridges in the Negro being, if anything, a little more uniform in size than in the White; no ossific (epiphysial) nodules fusing with the surface; no definite delimiting margin; no definition of extremities. Phase II is also characterised by subequal horizontal ridges but dorsally there is distinct evidence of osseous activity, for the grooves between the hinder ends of the ridges are becoming obliterated by a new finely-textured growth of bone. A dorsal delimiting margin is beginning to form and take the place of the more or less apparent dorsal outline present even at adolescence. The ventral part of the symphysial face becomes more sloping or bevelled, a curious feature which will repay further study. In some cases there appears at this stage a bony epiphysial nodule at the upper extremity of the symphysial face. There is no delimitation of extremities. These two phases carry us to the twenty-second year of life. It is immediately after this that the perplexing variations occur.

As an introduction to the interpretation of the more obscure features which we shall meet with immediately let us glance over the characters of the symphysial face in No. 366, a male Negro of twenty-two years (fig. 7). From this enlarged photograph one can see the growing dorsal margin and the dorsal platform developing alongside. The addition of bone to form this margin and the platform is very irregular. On the left side it is not thicker than 0.5 mm. On the right side the thickness is 6.5 mm. at the level of the upper nodule which is so clearly seen whereas at the lower end of the symphysis it is only 3.0 mm. The addition of this mass of bone naturally enhances the ventral bevel and where it exists it obliterates all sign of horizontal ridges and grooves. The ventral area of the surface shows a very finely honey-combed vascular surface upon which remnants of the ridges still remain. The question naturally

arises as to what is happening in the ventral part. I do not believe that any erosion has yet begun. There is no active destruction of bone but there is molecular disintegration of the ridges resulting from transformation of the surface. An upper nodule exists as yet only on the right side. It is plain that this nodule in itself does not define the upper symphyseal extremity. That delimitation will appear later and the distinction between the nodule and the real upper extremity will then make itself obvious. No suggestion of the lower extremity is present and the symphyseal face tends to follow down and fade out upon the margin of the sub-pubic arch as is the case in the Anthropoid. An upper nodule may of course never appear and the symphyseal outline is developed equally well without it.

The upper nodule of bone on the right side of No. 366 may justly be compared with the median bar of Gorilla B 624 (fig. 6) of which it is the homologue and counterpart. Keeping this in mind we are ready to understand the condition present in No. 744, a male Negro of twenty-two years (figs. 8 and 9). The actual symphyseal face is younger in this specimen than in the last. The dorsal margin has not yet developed and nothing but a mere outline is present, such as one would expect in phase II. The epiphyseal upper nodule is already formed and fused so that it stands out in marked contrast to the ventral rampart and to the lower extremity which are both well developed. These are still, as it were, laid upon the surface of the pubic bone; they have not become a part of it as is the case with the upper nodule. Apart from the site of fusion of the ventral rampart and the lower nodule the horizontal ridges are still quite apparent. There is indeed nothing to indicate an age greater than twenty-two except the obtrusive epiphyseal extensions, namely the ventral rampart and the lower nodule. Now this specimen presents two problems. The first is the meaning of the early appearance and vivid delineation of the rampart and the lower nodule; the second is the correct evaluation of the several features of the symphysis in relation to age. Should one, for example, depend upon the very obtrusive rampart as an indicator or should one rely upon the condition of the dorsal margin? In practice I find that these are the two problems which dog one's steps throughout this study of age characters of the symphysis. No better specimen than No. 744 could be presented for elucidation of these problems.

The ventral aspect of No. 744 shows well the thickness of bone laid down in the ventral rampart. Just below the upper nodule, at the point where the delimiting line veers suddenly outward toward the tubercle, the thickness of this new bone is 9.0 mm.; at the level of the lower extremity of the symphysis it is 6.0 mm. No bone has been deposited on the dorsal part of the surface consequently the bony thickening merely fills up the ventral bevel remaining from adolescent times. There is no doubt about the Primate character of the bone deposit in this specimen. We have here a median bar, albeit split into two ventral ramparts, even better developed than in the Gorilla B 624.

Naturally one does not expect to obtain often so striking an example as



No. 744, any more than one anticipates finding an Anthropoid so fortunately apposite as B 624. But having seen these bones one has no hesitation in interpreting the much more frequent condition of the human symphysis as exemplified by No. 860 of age twenty-three (fig. 10), a male Negro like the rest. The features characteristic of No. 744 are again apparent here but are not nearly so prominent. Even a specimen like this is comparatively rare in the White series, at least at so young an age, and would have been classed in my former work under the heading of a sporadic precocious attempt at rampart formation. So far as Man is concerned the interpretation is undoubtedly correct but clearly this precocious rampart formation is also a typical Primate feature undergoing retrogression though not so retrogressed here as in the majority of human specimens. It should be particularly noted that, in conformity with the age, the dorsal margin is barely beginning to form and there is no evidence at all of the lower extremity. The reader must not confuse the upper nodule present here with the later clearly defined upper extremity.

There are three factors responsible for the development of a margin round an articular surface and these come into play at very different periods of life. The first is the deposit of bone forming a basis or platform upon which the future plainly delimited surface will be fashioned. This factor is at work in the upper extremity of the symphysis at twenty-two. It is seen in No. 860. The second factor makes its presence felt at the site in question towards the end of the third decade. By it the rather shapeless mass of the upper nodule is remodelled into a clearly outlined upper extremity for the symphysis. The third factor does not appear at the symphysis until about forty-five. It is responsible for the definite rim which moulds up the margin into a somewhat sharp outline known to clinicians as lipping. In a later communication I shall have a good deal to say about this lipping which is not a pathological feature at all but an age feature of tolerable constancy. Of course the term pathological is open to considerable variety of interpretation; by it I refer to a physical change in the bone brought on and directly induced by disease.

In this specimen No. 860 one would not be so liable to a misjudgment of age through the appearance of the ventral rampart for it is obviously retrogressive and the lack of even an attempt at a lower extremity is perfectly evident. Nevertheless one cannot emphasise too strenuously or too frequently the necessity of pinning one's faith to the real pubis itself for indications of age, and not to any variable and retrogressive epiphysial structure. I realise very well the importance of this caution for the pitfall is one into which a careful observer may readily slip if he attempts to make a hasty decision.

A much more difficult specimen to interpret is No. 525 (fig. 11), a male Negro of twenty-two years. This has been described as accelerated in my previous work. The earlier discussion of this specimen (II, pp. 19-20) is quite significant and to this we must shortly return. At the moment however one recalls that a general acceleration of skeletal metamorphosis of about four years was accorded this individual. If the figure be examined attentively it



will be seen that the ventral rampart is simply a very retrogressive and consequently poorly defined example of the type of 744 and 860. The dorsal margin is not really formed nor is there any sign of the lower extremity. The upper nodule is indeed present as might be expected in any bone of this age but it is only the first of the three factors mentioned above which has so far been at work. The horizontal ridges are quite ill-defined; there is, one might say, a slovenliness though not a lethargy of bone formation but there is no real indication that the specimen is actually much older than his years.

We may now consider a specimen which exemplifies the last stage in the completion of symphyseal outline so far as this "anthropoid" strain of human pelves is concerned. The specimen chosen is No. 791, a male Negro of twenty-eight years (fig. 12). Here we have a symphyseal outline which in all essentials is completely developed. The dorsal margin and platform are clear. So is the lower extremity. The bony structure of the upper extremity and the ventral rampart are laid down although these features are not yet delimited in the finished manner characteristic of other parts of the outline. Further it is still obvious that both extremities and the ventral rampart have been developed from a new growth of bone laid down upon but not an integral part of the pubis itself. The ventral aspect indeed shows plainly a delimitation between these parts and the pubis. It also indicates the continuity of these parts through the lower extremity with the subpubic extension of the epiphysis of the ischial tuber. In my previous work No. 791 has been cited as an example of skeletal acceleration with contradictory features (II, p. 22) because, taking for the moment only the pubic characters, the symphyseal outline is completed in specimens of about thirty-three years, yet this completion in No. 791 does not harmonise with the granular appearance of the symphyseal face itself. The reason of the disharmony now becomes clear. It is the result of retention of an anthropoid strain relatively unusual in human symphyses.

#### *Effect of the anthropoid strain upon phase sequence in the Negro*

It is necessary now to consider modifications brought about by the anthropoid strain in the regular phase sequence of the Negro.

Among the fifty-two Negro male pelves of known age between seventeen and thirty-one years inclusive there are thirteen showing an undoubted anthropoid strain. This first makes its appearance at twenty-two years with the precocious (for Man) development of a ventral rampart. After thirty-one years the distinction between the anthropoid strain and the more typical human sequence becomes obliterated since the human sequence has by then caught up with the other type. The thirteen pelves in question are the following:

Age 22. Nos. 525, 744.	Age 26. Nos. 190, 809.
23. „ 860.	28. „ 791.
24. „ 857.	29. „ 568, 569.
25. „ 458, 764 (vi. fig. 4).	30. „ 343.
	31. „ 448.

Of these No. 525 shows about four years' acceleration and No. 764 about four years' retardation in symphysial appearance. Now the phase sequence typical for the male Negro has been previously defined but for convenience the leading features should be restated.

Phase I. Age -19. Typical adolescent ridge and furrow formation with no sign of margins and no ventral bevelling.

Phase II. Age 20-22. Foreshadowing of ventral bevelling with slight indication of dorsal margin.

Phase III. Age 22-24. Progressive obliteration of ridge and furrow system with increasing definition of dorsal margin and commencement of ventral rarefaction (bevelling).

Phase IV. Age 25-26. Completion of definite dorsal margin, rapid increase of ventral rarefaction and commencing delimitation of lower extremity.

Phase V. Age 27-29. Commencing formation of upper extremity with increasing definition of lower extremity and possibly sporadic attempts at formation of ventral rampart.

Phase VI. Age 30-33. Development and practical completion of ventral rampart with increasing definition of extremities.

Phase VII. Age 33-38. Changes in symphysial face and ventral aspect of pubis consequent upon diminishing activity, accompanied by bony outgrowths into pelvic attachments of tendons and ligaments.

Phase VIII. Age 39-45. Smoothness and inactivity of symphysial face and ventral aspect of pubis. Oval outline and extremities clearly defined but no "rim" formation or lipping.

Phase IX-X. Age 45- . . . Development of "rim" on symphysial face with lipping of dorsal and ventral margins. Erosion of and erratic, possibly pathological, osteophytic growth on symphysial face with breaking down of ventral margin.

For pelves of the anthropoid strain the second period, namely that during which the symphysial outline is built up (see iv, p. 63) is strangely jumbled and the phase sequence is actually inverted, phases IV, V, VI appearing in exactly the reverse order. It is this inversion which may be the cause of confusion in interpretation if the investigator is unwary.

A study of the pelves just enumerated shows the following features of phase sequence. At twenty-two the ventral rampart begins to form but not yet to fuse with the pubis. At twenty-three fusion of the rampart takes place. At twenty-four changes occur in the symphysial face itself and the upper epiphysial nodule begins to assume the character and outline of an upper extremity. These features continue to become more strongly marked during the twenty-fifth and twenty-sixth years during which time also the lower extremity makes its appearance. At twenty-eight fusion between the epiphysial structures and the true pubis is so thorough that there is commencing obliteration of the earmarks of the original anthropoid strain. This obscuration continues until thirty when it is almost fully developed. At thirty-one the ventral

margin becomes strictly delimited through the influence of the second factor in articular outline definition discussed on a previous page. Stating these features in terms of the phase sequence we find that phase VI begins at twenty-two, phase V at twenty-four and phase IV at about twenty-six. Phase VII follows at twenty-eight and phase VIII at about thirty. As a matter of fact these age relationships are not far from the probable age relationships in the giant Anthropoids although we cannot enter into a full discussion of this matter at the moment.

Comparing the statement of phase in the anthropoid strain with that typical of Man as enumerated above we find that phase III and phase IV, being defined by features of the pubis itself, occur in their normal order and at the regular time as in other human pelves. The dislocation in phase-age relationship is brought about by the retention of a comparatively well developed median bar (ventral rampart) and upper nodule. Reference to the key specimen Gorilla B 624 (fig. 6) will make this clear.

Certain anomalous features in the regular phase sequence as originally defined now begin to appear in their true light. For example, the troublesome manner in which the upper extremity sometimes becomes defined as soon as or even sooner than the lower extremity is obviously due to an "anthropoid" influence. The sporadic early appearance of the ventral rampart is explicable upon the same basis. These matters must receive further attention after we have investigated the more typically human series of Negro symphyses.

#### *The regressive type of Negro symphysis*

In the foregoing pages we have considered a type of symphysis showing distinctly a form of metamorphosis which is nearly related to and clearly a variant upon the anthropoid type. It is however inconceivable that so profound a modification as permanent separation of the pubic bones could occur without some marked concomitant changes discernible in human symphyseal metamorphosis. I am therefore about to present the type of symphysis which illustrates most definitely the peculiar human features of this curious bony change. Of the fifty-two pelves at present under consideration twenty-nine may be classed as being typically human. But upon the macerated skeleton there is no gross symphyseal difference between anthropoid and human types until the age of twenty-two years so we may rule out from the present group the ten pelves of an age less than this. The remaining nineteen are the following:

Phase III.	Age 22. No. 366. Accelerated to 24.
	703. Accelerated to 24.
	765. Retarded to 19.
23. No. 506.	Typical (n. fig. 11).
	782. Typical.
	792. Retarded to 19 (vi. figs. 10-11).
	850. Typical.
	862. Typical.
	874. Accelerated to 25.



- Phase III.                   Age 24. No. 497. Retarded to 22.  
                                       523. Retarded to 19.  
                                       524. Typical (but with lower epiphysis (vi. figs. 12-13)).  
                                       858. Retarded to 20.  
                                       27. No. 379. Retarded to 25.
- Phases IV and V.   Age 28. No. 474. Retarded to 25.  
                                       658. Retarded to 24.  
                                       778. Retarded to 25.
29. No. 259. Retarded to 26 (ii. fig. 15).  
                                       402. Retarded to 25 (ii. fig. 14).

The original phase sequence was defined, it will be recalled, for male White pelves and no alterations were made for the Negro except such as seemed clearly indicated. Since the original observations were made we have added about two hundred skeletons to the collection and these have naturally rendered some modification for the Negro advisable although one would hesitate to make any dogmatic and precise statements as yet. One notes the small accelerations and retardations of a couple of years or so and may ignore them. No marked accelerations can occur among this list for it has been shown that such accelerations were due to the anthropoid strain. The striking feature of the list is the increasing number of retardations of several years duration, three or even four. The five year retardations have already been discussed in my former writings (ii), but it is these smaller retardations, becoming rapidly more frequent until all symphyses of ages twenty-seven to twenty-nine are included, which arrest the attention and demand explanation. Phases III and V commence at the expected time; phase IV is delayed two years. There is no delay in phase VI since it is shortly after thirty years that this type of symphysis catches up on those of the anthropoid strain. As a matter of fact this series shows very well the delay characteristic of the human pubis in entering the second period of symphyseal metamorphosis during which the actual outline is built up (iv, p. 63).

Concerning the precise manner in which the outline is developed it is unnecessary to enlarge. In formation of the upper extremity a special epiphyseal bony nodule may or may not take part. There is no essential difference from the appearance of No. 525 or No. 860 (figs. 10, 11). The lower extremity is formed by delimitation largely on the pubic bone itself, and the ventral rampart by the linkage of independent bony nodules or by gradual accretion of new bone upon the eroded, bevelled ventral area. These processes have already been fully described and figured (i, pp. 306-308; ii, p. 8). The reader is referred particularly to a discussion of variations in type of symphyseal metamorphosis the accompanying figures of which are large and render more easy the interpretation of the more numerous illustrations in the body of the work (vi, pp. 410-413).

*Negro symphyses of intermediate type.*

It is possible that the preceding pages may have served to render still more obscure the problem of the symphysis. There is no mental tidying up without the use of "pigeon holes" and there can be no adequate final synthesis without a preliminary and searching analysis. I am therefore about to complete this analysis as far as we may carry it at the moment by presenting a series of pelves which defy assignment to either of the two groups so far considered. Of the forty-two Negro male pelves in question these number ten. The peculiar feature of these symphyses is that they invariably show some evidence of a rudimentary or spasmodically developing ventral rampart at an unusually early age for Man. This of course can have no other meaning than an origin from the anthropoid strain type of symphysis. Yet the vestiges of rampart are unrecognisable as such without previous knowledge of the first group which I have considered and figured in this communication. The sporadic occurrence of attempts at formation of a ventral rampart has been allowed for in my initial definition of phases and therefore it is possible to assign each symphysis to the phase-age scheme originally established. The complete list is the following:

Phase III.	Age 22. No. 413.	Typical (vi. figs. 14-15).			
Phase IV.		846.	Accelerated to 25.		
Phase V.	Age 26. No. 435.	Accelerated to 28.			
		859.	Accelerated to 28.		
	27. No. 716.	Typical except for rampart vestige.			
	802.	"	"	"	(II. fig. 13).
	28. No. 855.	"	"	"	
	29. No. 563.	"	"	"	
	30. No. 326.	"	"	"	
	598.	Retarded to 24.			

In accordance with their acceleration No. 846 becomes classified in phase IV, and Nos. 435 and 859 in phase V.

*Phase and age relationships of our Negro male symphyses of the third decade*

From the analysis just made it is possible to interpret the appearance of symphyses characteristic of the third decade much more intelligently and accurately than upon the baldly sketched outline hitherto published. There are undoubtedly two well marked types of symphysis easily referable to the anthropoid and regressive human strains. In addition there are always some for which the precise assignment is not so simple. These are really degenerate members of the anthropoid strain which however have not become so regressive that their symphysial features can be appraised with ease as in the case of the other two groups. Of the forty-two pelves between twenty-two and thirty-one years under consideration, thirteen belong to the anthropoid strain, nineteen to the regressive group and the remaining ten to the intermediate type. Since

these last ten are derivatives of the first group it follows that the anthropoid and regressive types are almost evenly divided among our male Negroes.

Of course one might classify all the pelves as closer to or more remote from the typical Eutherian metamorphosis. In this case the anthropoid strain would come first, the intermediate type next and the regressive group last. Armed with a fairly comprehensive knowledge of the mammalian symphysis, it is much easier to classify and evaluate the several features of human symphyseal metamorphosis to-day, than it was in the early stages of this survey. Nevertheless it is also fair to say that the original classification of the Negro symphyses was far more difficult than the arrangement of the Whites. As will be apparent later this difficulty in the Negroes did not really arise from a greater admixture of types but from a more abrupt differentiation of types which did not permit the slurring over of intermediate forms. Had one attempted in the first place to formulate a phase-age relationship from our male Negroes I am convinced that only bewilderment would have ensued. In the course of the next few pages I shall present evidence whereby the White symphyses may be analysed into the three divisions which we have been able to distinguish so clearly for the Negroes. Doubtless it will occur to the reader that with three different groups of symphyses each having a somewhat particular phase sequence and its own time relationship which is not steady for all three, there is little hope of arriving at a prediction of age for any individual pelvis. In this connection it must be remembered that, unless it is absolutely unavoidable, the symphysis should never be used alone; that the age prediction is at best an approximation; and that the most sanguine would not expect the prediction to be accurate to within less than two or three years if founded upon the entire skeleton, or to within less than five years if founded upon the pelvis alone.

In the tables recounting the several members of my three groups, I have given some data from which it can be deduced that the lee-way of five years for age estimation of the pelvis alone is ample for any skeleton of the third decade. It is also ample for any skeleton of less than fifty years but after that age the symphysis becomes distinctly less valuable as an age indicator.

The problem upon which we set out in this chapter was the synthesis of three types of symphysis into a phase-age scheme which does not involve too much detail to carry conveniently in mind when examining skeletons. Now this is precisely the problem upon which I set out several years ago and the scheme which I have restated in this communication is the final one decided upon for general purposes. If the reader use this he must in the first place, expect only an approximation correct within five years; secondly he must allow for the sporadic occurrence of a precocious (for Man) attempt at rampart formation; thirdly he must recognise the possible inversion of order of phases IV and V. With these points in mind it will be clear to the reader that my original phase-age sequence rests upon an extensive experience of all three types in both human stocks but more especially in the Whites. A con-



densed summary of the statements made in this paper may be arranged as follows, and from this it will be clear that my phase sequence is most closely bound to the regressive and intermediate groups; for the anthropoid strain was conjectured to be an anomaly in Man, a view essentially corroborated in the ensuing investigation of which this communication records a part.

Group		Commencement of phase in years			
Male Negroes	...	III	IV	V	VI
Anthropoid strain		22	26	24	22
Intermediate	...	22	25	26	30
Regressive	...	22	28	28	31

### *Groupings in the male White symphyses*

In the male White series there are thirty-eight pelves of ages from twenty-two to thirty years inclusive. We have none of the age of thirty-one. These thirty-eight symphyses present no difficulty comparable to that of the Negro males. Twenty-five of them are at once allotted to the regressive group; nine show the anthropoid strain and four only belong to the intermediate type. So closely indeed do the intermediate symphyses simulate the true regressive characters that, when grouping the White pelves in my former communication (I, pp. 328-329), I made no special reference to them. The anthropoid strain did cause me greater difficulty and after much thought I decided to give them up for the time being, merely remarking that in spite of their obvious location in the table they show some aberrant features which I briefly defined. Three of the skeletons I withdrew temporarily from the series of known age pending further inquiry. These are Nos. 653 of the age of twenty-six, 310 and 618 both of the age of thirty. The remaining six I have called examples of the mingling of phases, and I state that "these notes (i.e. upon the phase mingling) are not found on specimens of more than twenty-nine years" (I, p. 329). This observation now comes to have an important and striking significance. It has been shown that shortly after thirty years the regressive type of human metamorphosis catches up on the type showing an anthropoid strain and that obliteration of distinctive features in grouping thereafter rapidly disappears. The strange and hitherto inexplicable absence of phase mingling thus obtains an adequate solution. It is true that after thirty-nine years retardation of metamorphosis becomes the striking feature and the phase characteristic of the age supervenes upon the previously incomplete stage. This is another question which must be reserved for future consideration but which also finds ready interpretation by reference to the facts of Eutherian symphyseal metamorphosis.

It is unnecessary to dwell at present upon the particular features of the regressive group of White symphyses, but I do wish to make a careful distinction between the regressive group as a type of human metamorphosis and a *retrogressive* individual symphysis. The regressive group is an undoubted type and is the characteristic type of symphyseal metamorphosis among Whites.

It is only in a somewhat less degree characteristic of the Negroes. Occasionally there is found within this group, and among Whites more frequently than among Negroes, a specimen in which, even in the early twenties, the bony conformation seems indolent. There are few, low or ill-defined horizontal ridges; the extremities, especially the upper, are poorly formed or not defined at all; the ventral rampart is permanently incomplete, irregularly formed or barely distinguishable from the rest of the symphyseal face. Such a specimen is obviously even more degenerate than the regressive type and represents a stage still further removed from the general Eutherian form. This is a retrogressive or plainly degenerate symphysis. It is often but not necessarily associated with some anomaly in shape of surface contour of the symphysis and is particularly liable to mislead the observer who is not on the alert for its occurrence. I have figured it several times and examples are to be found in the female Negro No. 226 (VI, fig. 24) and in the male Whites No. 575 (I, fig. 17) and No. 317 (I, fig. 67). One curious peculiarity of this retrogressive form is that it occurs in the anthropoid strain as well as in the regressive group. Examples have been recorded in the male White No. 649 (I, fig. 61), and in the male Negro No. 525 (this paper, fig. 11). They must not be confounded with plain retardation such as is shown in No. 764 (VI, fig. 4). The occurrence of the retrogressive symphysis in both the anthropoid strain and the regressive group emphasises still further the real distinction between these two definite types of human symphysis, either of which may equally show degenerate forms.

Let us glance for a moment at the examples of anthropoid strain among male Whites in the third decade. They are the following:

Age 22. No. 256 (II + VI).	Age 26. No. 653 (New).
649 (II + V).	29. No. 436 (V and VI).
24. No. 667 (III + V).	30. No. 247 (VIII).
25. No. 267 (IV + VI) (figs. 13, 14).	310 (New).
	618 (New).

In all these is an "admixture" of phase V or VI except in No. 247 which, as would be expected of the anthropoid strain at this age, is already quiescent and in phase VIII. The three marked "New" are now added to the list of pelves of known age for the first time. It is the unexpected and formerly inexplicable early appearance of the upper extremity (phase V) or ventral rampart (phase VI) which is the undoubted earmark of the anthropoid strain.

The intermediate type is represented in the third decade of our male Whites by four examples to which no particular reference has been made in my original classification (I, p. 328), but have all been figured, as stated below, for the purpose of identification at the proper juncture. This time has now arrived and the reader is referred to my former work for the details of their form. In each the anthropoid strain, though obscure, can now be identified. They do not constitute anomalies when properly interpreted but by their very indeterminate character indicate their "anthropoid" origin.

Age 26. No. 490 (I. fig. 20).

27. No. 491 (I. fig. 22).

614 (I. fig. 21).

30. No. 360 (I. fig. 33).

*Relative frequency of the types in Whites and Negroes*

In résumé there are, among eighty pelvises of male Whites and Negroes between the ages of twenty-two and thirty-one inclusive, forty-four of the regressive group, twenty-two showing the anthropoid strain and fourteen of the intermediate type. These are distributed in the following manner:

	Anthropoid strain	Intermediate type	Regressive group	Total
White male ...	9	4	25	38
Negro male ...	13	10	19	42

On the face of these figures there is not enough evidence to conclude that the regressive group is much more characteristic of the White or that the Negro presents a greater tendency toward the anthropoid strain. It is perhaps significant however that examples of anthropoid strain are much better marked in individual specimens among Negroes. Had the original survey been made first upon our Negro material it is possible that the characteristics of the several phases and their precise age-relationships would have presented far greater difficulties in classification. And it is certainly true that these very plainly marked indications of anthropoid strain in Negroes provide the connecting link between human symphyseal metamorphosis and the typical Euthirian sequence.

It is equally clear that the intermediate type of symphysis is the form which links up the regressive group with examples of the anthropoid strain and which renders certain the correct interpretation of the former.

*Relation of the types to acceleration and retardation of phase*

Several pitfalls, which present themselves in the course of age determination by reference to symphyseal phase, have been discussed already, and indeed the one now to receive attention has had passing notice. It is this. Acceleration and retardation of metamorphosis at the symphysis are not terms corresponding to the anthropoid strain and to the regressive group respectively. Each type itself has a modal age relationship for the successive phases; these have been pointed out. But in each type there are certain specimens which leap in front of or lag behind the modal rate of progress in metamorphosis. No better examples could be used than Nos. 525 (fig. 11) and 764 (VI, fig. 4). Assuming that No. 744 (fig. 8) represents the modal appearance of the anthropoid strain in Negro symphyses of twenty-two years, then No. 525 is plainly accelerated. The ventral rampart is not only formed but is so fused with the pubic bone as to be practically indistinguishable from it. On the other hand No. 764, though of the age of twenty-five, has only an imperfectly formed ventral rampart. These two specimens deserve a little closer inspection.



No. 525 is distinctly anomalous in several respects. The surface is saddle-shaped on the left bone, biconvex on the right. The dorsal margin on both sides is complete in the upper half but almost lacking below. The symphyseal surface itself has a waxy appearance upon which the ridges are present but are ill-defined. In other words the specimen is a retrogressive example of its type and the retrogressive appearance of the surface is associated, as so often happens, with anomaly in outline and in surface contour. The ventral rampart has grown irregularly on both right and left pubic bones, and is imperfectly separated from the rest of the surface. The upper extremity of both sides is completed, the lower extremity is not. The features of this specimen, on being analysed, are all indicative of the anthropoid strain but the appearances are by no means typical. For its age it is retrogressive as far as the anomalous outline and contour and the faintly marked ridges are concerned. It is accelerated however since fusion between rampart and pubis proper does not usually reach the stage here presented at the age of twenty-two years even in examples of the anthropoid strain. This skeleton has received notice in a former discussion (II, pp. 19-20); it comes from a man who died of pneumonia in our own wards at City Hospital. There is no doubt whatever about the correctness of the age record. Other bony features, the closure of the cranial sutures, the condition of the clavicles, and the vertebral epiphyses suggest an age of about twenty-six or rather more. This suggested age would be the one fitting the actual condition of the symphysis and hence the skeleton in general shows an advanced stage of bony metamorphosis for the real age of twenty-two years. In addition to the acceleration of skeletal metamorphosis in general, and so far as I know at present in no way related to this acceleration, the symphysis pubis belongs to the type which I have called the anthropoid strain.

No. 764 does not present nearly so difficult and involved a skeletal picture. Here there is no anomaly of outline or of surface contour. Further there is nothing of particular note in the general skeleton as the sternal epiphyses of the clavicles are not yet completely united and the epiphyses of the vertebrae and of the ribs are already fused. The ventral rampart is forming on the symphyseal face but it has not reached the state of perfection shown in No. 744 which is three years younger. The upper and lower extremities are forming with the aid of nodules, the development of which from the horizontal ridges of the ventral bevel is very clearly seen. The essentially greater age of this specimen is disclosed however, by the fact that a dorsal margin and platform are almost completed by resolution of the horizontal ridges and furrows into a more or less uniform surface of a finely pitted vascular appearance. One might with justice ask why this specimen is not one of the intermediate type. The answer is far more easily given by demonstration than by description. One may define the symphyses of intermediate type as exhibiting a rudimentary or spasmodically developing rampart; this is so natural a description of the appearance that in the earlier work symphyses of intermediate type were thus classified. The case in point, No. 764, however shows a perfectly well developed rampart independent of the rest of the pubis and could be taken for a normal example of the anthropoid strain were it not for the discrepancy in

the stages of development of the rampart on the one hand and of the dorsal margin and platform on the other.

One might go on multiplying cases of acceleration and retardation but that is unnecessary; the two examples quoted give all the salient and crucial features to which attention should be drawn. Neither is it necessary to discuss features of acceleration and retardation in the more obviously human regressive type of metamorphosis; these have been dealt with on former occasions and have been copiously illustrated. There is, however, another point to which in conclusion we should devote a few moments, namely the relative importance of the several features of the symphysis as age indicators.

*Relative importance of the several symphyseal features as age indicators*

In presenting the evidence in favour of an anthropoid strain in human symphyses I have emphasised the necessity of a correct evaluation of the various symphyseal features as age indicators. I raised the question as to whether one should depend more upon the very obtrusive rampart as an indicator, or upon the condition of the much less striking dorsal margin and platform. It is well to be quite clear about this.

I have shown that the distinguishing features of the anthropoid strain are exhibited in the epiphysal remnants which together make up the ventral rampart and upper extremity, and also to a less extent, the lower extremity. These epiphysal remnants are especially well marked in the intermediate type and even in the regressive form of human symphysis although in these they are neither so pronounced nor so independent of the actual pubic bone itself. One might, and indeed would, classify the three types as stages of retrogression were it not that the first and third, at least, exhibit particular retrogressive forms which can be distinguished the one from the other. Now it follows that, in spite of their bolder character, the epiphysal remnants are less stable and less reliable as age indicators than the features of the pubic bone proper. I have given the phase-age relationships for the three types of metamorphosis in the foregoing pages and these tables show plainly how inadvisable it is to pin one's faith to these as age determinants without a very careful examination and strict discrimination between the types. Correspondingly elaborate precautions are not necessary in age estimation drawn from a study of the pubis itself since such variations do not occur.

The phases as defined earlier in this communication depend mainly for their elucidation upon features of the pubic bone and not of the epiphysal remnants although it is true these cannot be entirely ignored. Phases I, II, III depend upon the pubis alone. Phases IV, V and VI may or may not involve epiphysal formations as separate entities; both extremities may be developed without the appearance of a definite nodule and the ventral rampart may grow by simple accretion of bone upon the ventral bevel without the formation of bony bridges or other indications of a separate bony element. It must be carefully observed that in my definitions I do not lay stress upon the formation of bony nodules for extremities or rampart but rather upon the *delimitation* or increasing definition of these features. The essential principle



of age determination by means of the symphysis is therefore based upon the permanent characters of the pubic bone and not upon the epiphysial features which are variable in occurrence and in time relationship.

The figures which illustrate this paper are from photographic studies by Miss Helen F. Harvey. In view of the fact that Miss Harvey has now taken up other responsible duties befitting a woman's career it is becoming that I make some acknowledgment of the very unusual impetus which she has given to anatomical photography in its various aspects. Those who have seen her colour work and stereoscopic projection can never forget the debt of gratitude which students and teachers of anatomy owe to Miss Harvey for her ingenuity and skill in developing these processes to so fine a pitch of excellence and at the same time to so simple a technique that they must be used in all modern anatomical equipments of the next decade.

### *Summary*

1. The human pubic symphysis presents a Eutherian metamorphosis in modified form as a result of the permanent separation of the two pubic bones.

2. Pubic metamorphosis in the giant Anthropoids is the connecting link between the human and the more typical Eutherian form. The epiphysial remnants of the human symphysis, namely ventral rampart, upper extremity and to a less and more variable extent the lower extremity, are the homologues of median bar and upper and lower nodules of typical Eutherian metamorphosis.

3. Among human symphyses, both White and Negro, there exist two well defined types of metamorphosis. The first has the epiphysial remnants obtrusively developed with consequent modification and even inversion of the phase-age relationship as originally enunciated. The second shows little or no independent epiphysial formation and is the modal type in both human stocks. The first of these types is clearly related to one form of metamorphosis as shown in the giant Anthropoids and therefore is called the anthropoid strain. The second is named the regressive type of human metamorphosis. Between these two modes there is an intermediate type of metamorphosis which serves to link the other two.

4. The three types occur in Whites as in Negroes but are more strikingly distinguished in the latter. There is no great difference in relative frequency.

5. Examples of both the anthropoid strain and the regressive type may be accelerated or retarded in time relationship and such examples differ in their exact features according to the type to which they belong.

In addition actual retrogressive examples of each type occur; these often present anomalies of outline or of surface contour in addition to the retrogressive features of the symphysial face.

6. In estimating age by the symphysis one must be cautious in evaluation of the several symphysial features, those of the pubic bone itself being much more reliable than the various epiphysial remnants. If the type is clearly distinguished however these remnants are of distinct help in coming to a correct conclusion.



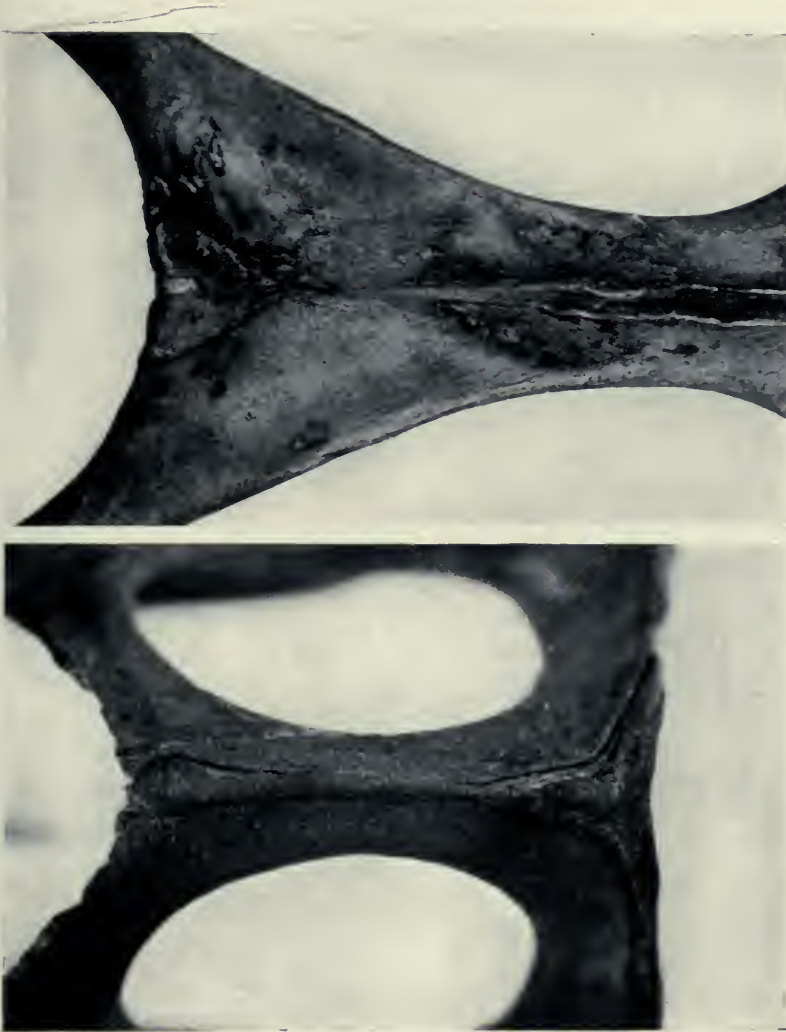


Fig. 2. Symphyseal area (upper part) of young adult *Macropus bennetti*, B 181, W.R.U., ventral aspect  $\times 2$ . Observe well defined upper nodule. The median bar exists merely as a median disc between the symphyseal faces.

Fig. 1. Symphyseal area of young adult *Peltaurus breviceps*, B 187, W.R.U., ventral aspect  $\times 6.5$ . Note the median bar with club-shaped upper and triangular lower extremities (nodules).

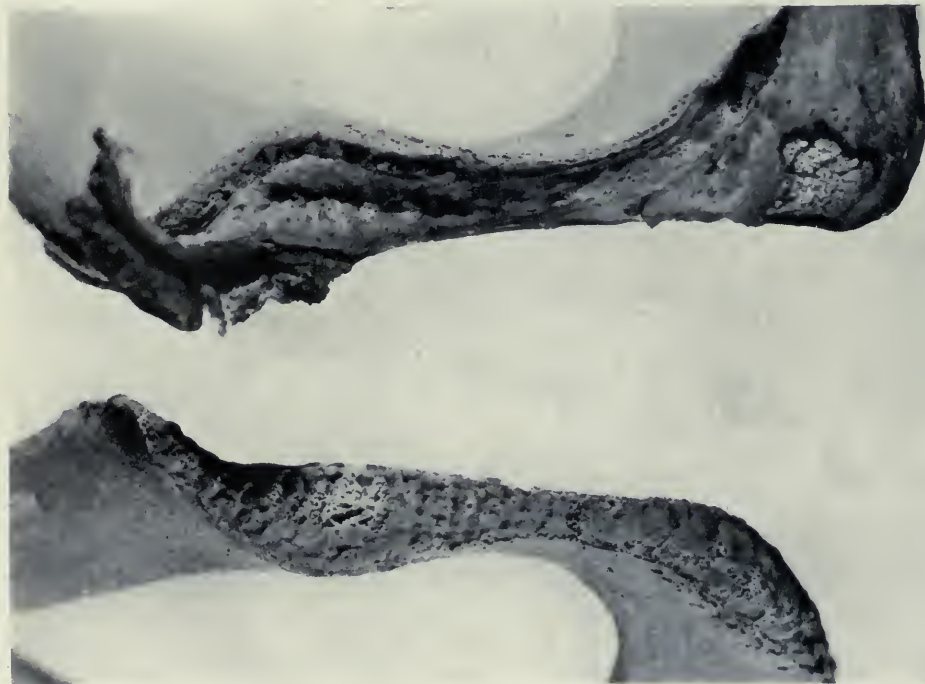


Fig. 3

Fig. 3. Symphyseal faces of young adult *Dendrolagus inustus*, B 193, W.R.U.,  $\times 2$ . The left symphyseal face is devoid of the epiphysal structures which are united by as yet non-osseous tissue to the right symphyseal face. The small upper nodule is obscured by the ligamentous base for the "marsupial bone." The median bar stands out clearly and the tongue which projects between the symphyseal faces is easily recognised. The lower nodule unites the ischial epiphyses of the two sides and hence in this specimen the left epiphysis is united to the right one on the right of the illustration.



Fig. 4

Fig. 4. Symphyseal area of young *Phascodomys tasmaniensis*, B 601, W.R.U., ventral aspect  $\times 2$ . The lower nodule is the first of the median structures to ossify.



Fig. 5. Symphyseal area of young adult *Odocoileus virginianus*, B 633, W.R.U., ventral aspect  $\times \frac{1}{3}$ .





Fig. 6. Symphyseal area of young adult *Gorilla gorilla* (Wyman), B 624, W.R.U., ventral aspect  $\times \frac{3}{4}$ . The left pubis is shown in face, the right in ventral aspect. Note the median bar with expanded upper nodule. There is no lower nodule, the median bar (broken) merely tailing off below.



Fig. 7. No. 366, W.R.U., Negro, male, age 22. Symphyseal faces  $\times 2$ . Note the developing dorsal margin and adjacent "platform." The right side possesses an upper epiphysis or nodule of considerable development. This striking feature is absent from the left side. The ventral area (towards centre of illustration) shows a bevelled, finely honey-combed, vascular surface on which, especially on the left, remnants of horizontal ridges can be seen.



Fig. 8. No. 744, W.R.U., Negro, male, age 22. Symphyseal faces  $\times 2$ . There is here no sign of the dorsal margin or platform. The epiphysial upper nodule, ventral rampart and lower extremity (nodule) are well developed but as yet appear to be lying on the actual pubic face.



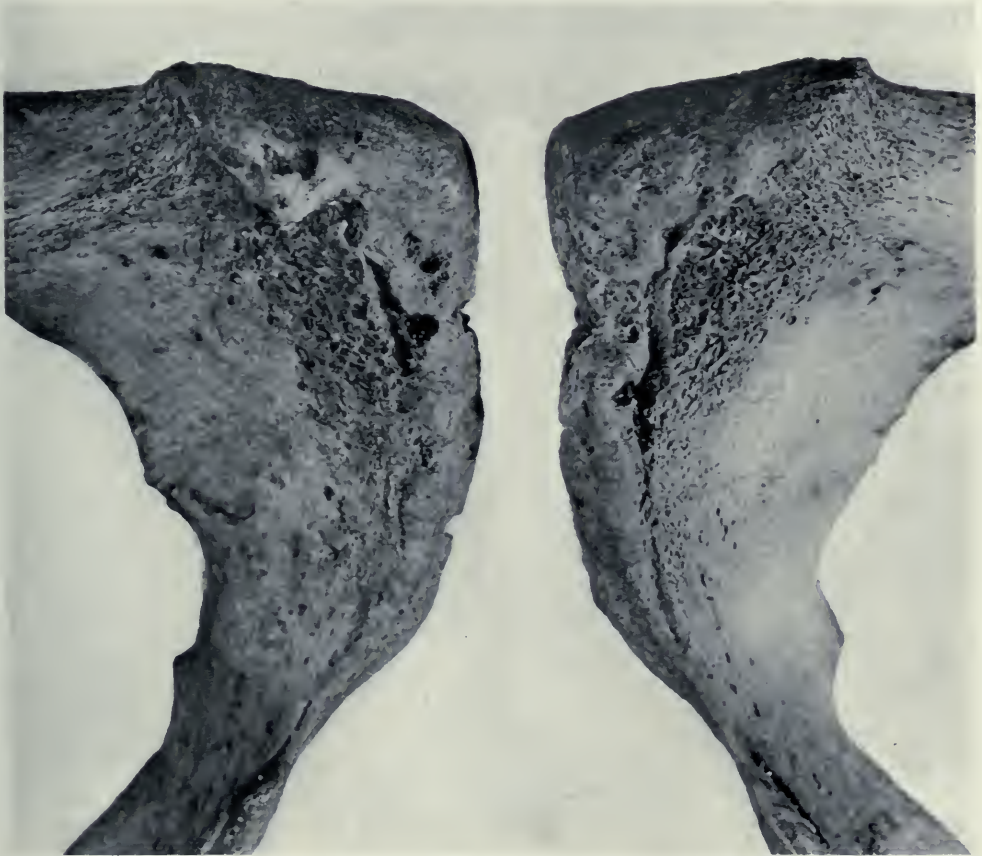


Fig. 9. No. 744 (compare Pl. VI, fig. 8). Ventral aspect of symphysis. Note the continuity of the epiphysial structures of the pubis with the epiphysis of the sub-pubic arch.



Fig. 10. No. 860, W.R.U., Negro, male, age 23. Symphyseal faces  $\times 2$ . On the horizontal ridges near the dorsal margin the transformation into a platform is beginning. Upper nodule, ventral rampart and lower nodule are present as in Pl. V. fig. 7, but much less plainly seen.



Fig. 11. No. 525, W.R.U., Negro, male, age 22. Symphyseal faces  $\times 2$ . On the horizontal ridges near the dorsal margin transformation of texture is commencing (cf. Pl. VIII, fig. 10). The ventral rampart and upper nodule are simply retrogressive and poorly defined examples of the type of Nos. 744 and 860. There is no lower extremity.





Fig. 12. No. 791, W.R.U., Negro, male, age 28. Symphyseal faces  $\times 2$ . This is late stage of the anthropoid strain just before final obscuration through fusion of the rampart with the pubic bone itself.



Fig. 13. No. 267, W.R.U., White, male, age 25. Symphyseal faces  $\times 2$ . This is an example of the anthropoid strain well marked for the White stock. It should be compared with Pl. VI, fig. 8 and Pl. VIII, fig. 10. Note the developing dorsal platform and the obtrusive ventral rampart with commencing definition of upper and lower extremities.

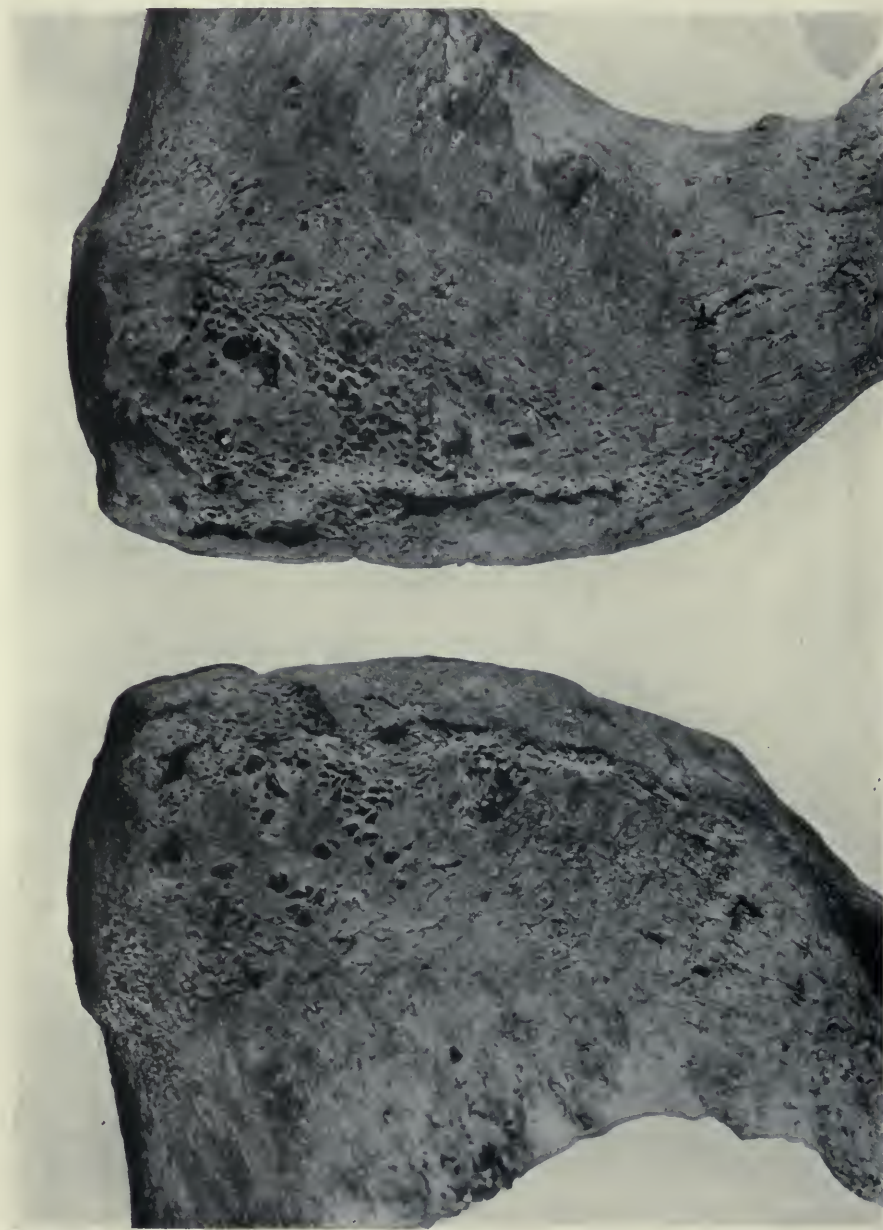


Fig. 14. No. 267, W.R.U., White, male, age 25. Ventral aspect of symphysis  $\times 2$ . This and Pl. XI, fig. 13 are companions. Note the amount of bone belonging to the ventral rampart. Compare Pl. VII, fig. 9.



# PRELIMINARY OBSERVATIONS ON THE NOSE OF THE AUSTRALIAN ABORIGINAL, WITH A TABLE OF ABORIGINAL HEAD MEASUREMENTS

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THESE observations are based upon (1) an examination of the bony nose in the aboriginal skulls in the Anatomy Department and in the Museum of Morbid and Normal Anatomy of the University of Sydney and the Roth series of aboriginal skulls in the Australian Museum together with various other European, South African negro, and Melanesian skulls, and (2) examination and dissection of the nose in two aboriginal heads. So far only one head (H. B. 1) has been dissected in full detail, but it is apparently a fairly typical specimen of the Australian aboriginal as regards the general features (see fig. 1).

With regard to the nose of H. B. 1, while its external features are typical, the bony nose deviates in one respect: the apertura piriformis is amblycraspedote, whereas most of the aboriginal skulls in our possession are bothrocraspedote or orygmocraspedote; otherwise the features are typical<sup>1</sup>.

The spine is only moderately projecting, thus bringing this skull into the lophacanthic group<sup>2</sup>.

As is commonly found in our series of skulls, the nasal bones present the typical depressed form, and the nose is platyrrhine.

At the end of this article is a table of anthropometric measurements of the two heads and of soft tissue thickness measurements for reconstruction work (Table A) together with definitions of the points used.

All the general data (e.g. skull measurements) are necessarily incomplete with the exception of the nose, as these observations are intended to be preliminary to a complete description of the facial muscles and other features of the two heads.

## EXTERNAL NOSE

As regards the external nose, the various measurements are to be found in Table A.

A clear idea of the nose may be obtained from the accompanying figures,

<sup>1</sup> Macalister (13) distinguishes four types of aperturæ: (a) oxycraspedote or European type with the sharp lower margin; (b) bothrocraspedote, with well developed fossa prænasis; (c) amblycraspedote, a type intermediate between these two; (d) orygmocraspedote, the anthropoid type with a smooth lower margin.

<sup>2</sup> Macalister in the same article distinguishes three types of nasal spine: (a) oxyacanthic, in which the spine is well developed (European type); (b) cryptacanthic, where the spine is rudimentary or absent; (c) lophacanthic, where the spine is intermediate between the above two

and accurate casts of the heads are preserved in the Anatomy Department, Medical School of Sydney University for future reference. These casts were made of printers' roller composition, a very elastic and durable material, giving perfect moulds of such structures as the ears, which are very difficult to obtain with plaster of Paris.

The aboriginal nose is remarkable for three things:

(i) The absence of any true tip to the nose, there being a convex ellipsoidal area instead of a true tip or point.

In the absence of a tip to the nose as a point from which to measure, an arbitrary tip was obtained in the following way: The curved alar margins of the nostrils (i.e. the medial edges of the alae) were continued medially in their



Fig. 1. Norma facialis of H. B. 1. (Photo.)

(All figures unless otherwise indicated are oriented in the Frankfort horizontal plane.)

curve until they met in the middle line. This medial point was found to be almost the most projecting point, and in these aboriginals was called the tip of the nose.

(ii) The great width and small height of the lower portion of the nose, i.e. that portion below the bridge. The nostril is remarkable for its wide lateral extent, so wide that the ala nasi lies completely lateral to the bony apertura piriformis, and also for the fact that it is possible to inspect directly the floor

of the nasal cavity through the anterior nares with scarcely any manipulation of the ala nasi.

Another feature brought out on dissection was the great development of the *pars transversa* of the *m. nasalis* and its probable moulding effect on the nose contour. This is indicated in fig. 3, where it will be seen that the skin thickens just below the rhinion, this being due to the great thickness of this muscle, which unites with its fellow of the opposite side to form a broad flat sheet of muscle over the cartilaginous dorsum of the nose.

(iii) The depressed bridge of the nose—this flattened appearance is due in part to the small and depressed nasal bones, but is accentuated by the broad fold of skin covering the *musculus oculo-buccalis*<sup>1</sup>, and the pad of fat in the areas extending from the bridge of the nose to the cheek and hereafter referred to as the naso-buccal gyrus. This gyrus seems to be a pronounced feature in the aboriginal and makes the bridge of the nose seem to be almost on the same plane as the face.

This type of nose is commonly seen in newly born white infants in which all three peculiarities are well marked.

#### THE MUSCULATURE OF THE NOSE

The nomenclature used by Eisler(7) has been followed.

The chief features observed in H. B. 1 were: (1) the great size and thickness of the *m. nasalis* both in its *pars transversa* and *pars alaris*; (2) the large and well formed *m. alaris nasi*. This arose mainly from the whole outer surface of the lateral crus of the *cartilago alaris major* and formed a continuous sheet of muscle (Henle, Eisler, Schwalbe). This sheet of muscle represents the anterior and posterior dilator muscles of Cunningham. (3) The wide lateral extent of the depressor septi portion of the *orbicularis oris* (see Poirier(14)). (4) The presence of definite *anomalus maxillae* muscles on both sides of the face. (5) We suggest that the musculature forms a nearly complete constrictor of the nose aperture not at the nostril, but laterally at the junction between the vestibule and the true nose cavity.

This "*orbicularis nasi*" (see, however, Eisler, pp. 145, 146) was further confirmed by tracing the relation of the edge of the bony aperture to the cartilaginous and movable framework of the nose, when it was found that the *pars transversa* followed closely the junction between the bony and movable portions of the nose. No trace of a *musculus apicis nasi* could be found.

#### MOVABLE FRAMEWORK OF THE NOSE

Turning now to the alar cartilages, septum, etc.

(1) The *cartilago alaris major* agrees with that of the American negro, in that the lateral crus does not run parallel with the medial as in most Europeans, but is bent up at a marked angle (fig. 3). This angle seems to be even

<sup>1</sup> The oculo-buccal muscle is a special development of fibres from the *orbicularis oculi* and extends down from the inner canthus to be inserted into the fat and skin of the cheek.



more marked than in the negro, judging by Schultz's figures(15). Kallius(10), however, figures (p. 126, fig. 7) a squat female European nose in which the two crura form an angle. It is evident from fig. 2, that the lateral crus of the greater alar cartilage takes little or no share in the support of the ala nasi, but acts as a basis of support for the m. alaris nasi.

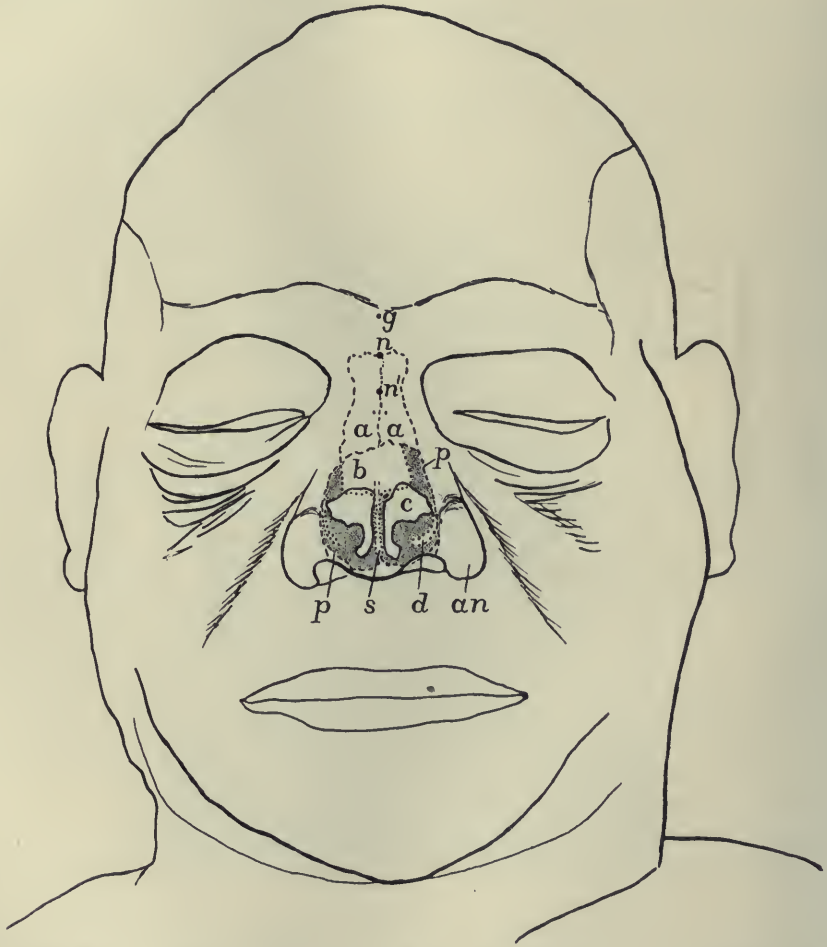


Fig. 2. Orthogonal projection of nasal bones and cartilages on the norma facialis of H. B. 1.  
*a.* Ossa nasalia; *b.* cartilago nasi lateralis; *c.* cartilago alaris major; *d.* cartilago alaris minor;  
*g.* glabella; *n.* nasion; *n¹.* pseudonasion; *an.* ala nasi; *s.* cartilago septi nasi; *p.* margin of  
 apertura piriformis.

Another very definite feature was the marked way in which the upper borders of this cartilage overlapped the lateral cartilage (figs. 2 and 3), an indication probably of the large size and mobility of the soft parts of the nose and of the anterior direction of the nostril. This, however, is seen in the white race (see Kallius, figs. 4, 6 and 7). Although the larger alar cartilages project

well beyond the septum nasi, as is the case in most negroes (fig. 3), yet we doubt if they were in contact, though possibly, as the result of dissection, we may have separated them to a greater extent than was actually the case in the living subject (fig. 2). The hinder pointed extremity of the lateral crus was 3 mm. anterior to the margin of the apertura piriformis on the right side and 4 mm. on the left side.

(2) The *lateral cartilages*, which are really expansions of the septal cartilage, approximate more closely to the quadrangular shape believed by Schultz to be characteristic of the white races (figs. 2 and 3).

(3) Nothing can be stated definitely regarding the frequency of the minor alar cartilages and the sesamoid cartilages (see figs. 2 and 3).

(4) As regards the *septal cartilage*, it will be seen from fig. 3 that it follows fairly accurately the contour of the nasal bones as far as the lower edge of the lateral expansions, and that immediately below this, it commences to curve downwards and backwards. The general outline of this cartilage is very similar to that figured for the negro by Schultz.

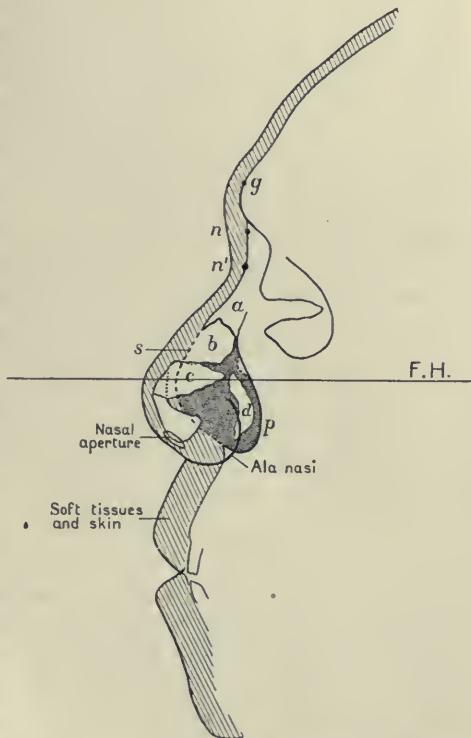


Fig. 3. Profile view of nasal framework and of external nose in H. B. 1. (Lettering as in fig. 2.)

#### THE RELATION OF THE EXTERNAL NOSE TO ITS BONY AND CARTILAGINOUS FRAMEWORK

The profile of the nose follows that of the nasal bones fairly closely, but over the septum nasi we see the soft tissues thicken owing to the great development of the pars transversa of the m. nasalis, whereas the procerus muscle in H. B. 1 seemed to have little direct effect in altering the contour over the nasal bones. The thickness of the soft tissues (see fig. 3) at the tip of the nose and at the nasal spine (·8 cm.) also exceeds the average found in white and negro (Schultz).

It is also immediately apparent from figs. 2 and 3, that the ala nasi lies almost completely lateral to the bony apertura piriformis and that its hinder border is a few millimetres anterior to the bony apertura in profile view. These facts are of value for reconstruction purposes. These figures also show that the nostril lies at the level of the lower bony margin of the aperture, and both in

the living and the dead aboriginal, it is a commonplace observation that the floor of the nose can be inspected through the anterior nares with scarcely any manipulation of the soft tissues of the vestibule, this condition being quite the reverse of the average white nose.

Schultz, in discussing the relation of the breadth of external nose to the breadth of the apertura piriformis, expressed the relation by an index,

$$\frac{\text{Breadth of aperture} \times 100}{\text{Breadth of nose}}.$$

This gives H. B. 1 an index of 62.4, slightly below the average found in the negro (Schultz).

Schultz says that "no conclusions concerning the breadth of the external nose can be drawn from the breadth of the bony aperture." He found even in the adult negro that the index varied from 53.2 to 78.9.

From an examination of photographs and of actual living aboriginals, we are of opinion that the index will be found to be always low and to vary to a much less degree than in white and negro noses. This is confirmed by Klaatsch (p. 70). As a result of this great width, we believe that the *alae nasi* will be found to lie very constantly lateral to the bony aperture.

#### AREA PRAENASALIS

As regards the bony apertura piriformis, we have little to add to the accurate descriptions of Macalister and Klaatsch. We had concluded a preliminary survey of a large number of Australian aboriginal and other skulls before we discovered Macalister's work. Our efforts were directed towards arriving at a satisfactory interpretation of the wide range of variation found more especially at the lower border of the apertura, from the smooth gutter-like anthropoid condition to the sharp knife-like margin found in the average European skull.

Macalister divides the bony margin of the apertura in the foetal European skull into four portions:

(1) The nasal bone edge; (2) the sharp lateral edge of the frontal process of the maxilla; (3) a smooth intermediate area; (4) the paraseptal line. These he traces in the adult skulls of various races. Looking at the skull in the lowest types, he recognised that the alveolar bone of the large prognathous incisor teeth in these races, rounded off the intermediate area and converted it into a smooth gutter leading from the nose on to the face, while at the same time the nasal spine was less developed and almost absent. He further recognised that in skulls of races somewhat higher in the scale, the intermediate area was converted into a pit or fossa, bounded posteriorly by the *paraseptal ridge* and a lateral continuation of it, which he called the *anterior dental ridge*.

This latter ridge runs to the lateral wall of the nose, near the inferior turbinate at its anterior end. It is often seen to be channelled and to contain the anterior superior alveolar nerves and vessels to the incisor teeth. Klaatsch called these combined ridges the *margo infranasalis*. Bounding this pit



anteriorly is another ridge which was not apparently named by Macalister, but which Klaatsch called the *crista prae-nasalis*.

We have used the following descriptive terms:

(1) *Margo infranasalis* formed by (a) *Anterior dental ridge*, (b) *Paraseptal ridge*.

(2) *Crista prae-nasalis* (or incisor ridge).

(3) *Area prae-nasalis*, which lies between (1) and (2) and is approximately the same as the fossa prae-nasalis or Macalister's intermediate area.

The term area is used, instead of fossa, as there are many orygmocraspedote (gutter-like) skulls, in which the ridges are so rudimentary that the area, while still distinct, becomes smooth and does not form a fossa. In aboriginal skulls, we find that the smooth gutter-like type of the apertura predominates; next comes a type in which the ridges are present, but the fossa is ill developed; finally we find the types with well-marked ridges and a true fossa. This latter bothrocraspedote form, is not so common as we had at first thought. Amblycraspedote skulls are very occasionally to be found.

The next feature we wish to emphasise is the remarkable variability of the above-mentioned ridges in aboriginal skulls. This was also remarked upon by Klaatsch. Thus we find skulls with the paraseptal ridges present or absent. Similarly with the anterior dental ridges and the cristae prae-nasales. The most constant ridges were the paraseptal ridges, next in frequency were the anterior dental ridges and the cristae prae-nasales in their lateral portions. In the aboriginal skulls available to us, we find the ridges completely absent, more especially (1) in young skulls up to 16-18 years of age, provided the alveolar prognathism is marked (example: Mus. N. and M. A., No. 1311) and (2) in many old skulls (as indicated by tooth-wear) (e.g. Mus. N. and M. A., No. 1308).

These cases are usually associated with a poorly developed nasal spine. Further we would remark upon the close approximation of the teeth to the nasal aperture, so that the average distance from the tips of the roots of the mesial incisor teeth, to the centre point of the medial end of the area prae-nasalis is only about 3 mm. This is a remarkably constant feature of a series of aboriginal skulls and has been partly emphasised by Klaatsch. In many skulls, the central incisor tooth of one side is missing and the alveolus partly absorbed, the tooth having been knocked out at puberty, in initiation ceremonies. In these skulls, on the side of the missing tooth only, the crista is less well-developed, and in closer apposition to the margo infranasalis, thus narrowing the area prae-nasalis and causing it to approximate to the condition seen in the amblycraspedote skull. We may remark here on a variation, seen by us in one Australian aboriginal skull, one Melanesian, and three African negro skulls. In these skulls, in spite of a considerable degree of alveolar prognathism (see fig. 4), the area prae-nasalis was apparently absent and the entrance to the nose was guarded by a fairly sharp margin, representing, we believe, the margo infranasalis. This margin, however, never became as sharp as that found in the typical oxycraspedote skull. Another African negro skull

in the Australian Museum approximated very closely to this condition (Aus. M., No. 1211). Now in all these skulls, we found that the distance from the tips of the roots of the incisor teeth to the margo infranasalis was very considerable (12–15 mm.). The significance of this will become apparent later.

Turning now to the influence of the softer tissues on the bone, from dissections of H. B. 1, we doubt if the depressor portion of the m. nasalis (called by Eisler the pars alaris) plays any part in the formation of the crista prae-nasalis. In examining the relation of the fossa or area prae-nasalis to the soft parts of the nose it was found that, approximately, the posterior wall of the vestibule was bound down to the area prae-nasalis by tough fibrous tissue. This has been confirmed by a histological examination of this tissue, when it was found not to be markedly vascular and to contain much fibrous tissue and fibro-cartilage.

#### INTERPRETATION OF THE VARIATIONS FOUND IN THE BONY APERTURA IN MAN AND ANTHROPOIDS

We believe that the variations found in this region of the bony nose, may all be interpreted as follows: The main factors moulding the bone are—

(1) The degree of alveolar prognathism with which may be coupled the amount of arching or curvature of the teeth. Thus we find some skulls with a marked arching of the bone from the nose to the alveolar margin, while in others which present marked alveolar prognathism the bone is yet fairly flat and straight, and the teeth are straight from biting edge to root apex.

(2) The second factor influencing the lower margin of the apertura is the distance from the tips of the incisor tooth roots to the margin of the apertura, or more accurately to the medial end of the chief diagonal of the oval prae-nasal area or fossa.

(3) The size of the teeth, their “set” or direction, and, of course, the pressure of the bite on them and its frequency of application. (These last factors are obviously almost incalculable at present.)

Correlated with the above factors is the arching or flattening of the anterior portion of the palate. In prognathous skulls, if the roots of the incisor teeth lie close to the lower margin of the apertura piriformis, the anterior portion of the palate is flattened but if the roots of the incisor teeth lie at a distance from the lower margin of the apertura piriformis, the anterior portion of the palate is arched.

In orthognathous skulls the anterior portion of the palate is arched, although the roots of the incisor teeth lie close up to the lower margin of the apertura piriformis.

(4) The shape and size of the vestibule of the nose, the posterior wall of which is adherent to the area prae-nasalis. We may call this the respiratory factor, and it is at present incalculable.

The influence of these factors may be outlined in the case of the crista prae-nasalis. The crista prae-nasalis is only developed in those skulls in which



the teeth, though prognathous, are less so than in orygmocraspedote skulls. At the same time the teeth must lie close up to the nose, or they must be so large and powerful that their pressure influences the lower margin of the apertura piriformis. Further evidence in favour of the cristae being closely correlated with pressure effects of the incisor teeth, is to be found in their absence in young aboriginal skulls, and in very old skulls. Again we see the reduction of the crista on one side in skulls where the tooth of that side has been knocked out at puberty. Again we have their reduction or complete absence in the exceptional skulls which have been mentioned above, e.g. those in which the distance from the tips of the incisor teeth to the nose aperture is over 1 cm. In these cases the large mass of bone between the teeth and the nose obviates the necessity for the development of a strut or crista prae nasalis. If, however, in these latter cases the teeth are very large and powerful, we may get a condition approximating to the orygmocraspedote skull, but with a fairly well-developed nasal spine, large paraseptal ridges and the crista while developed laterally, fades away medially. This is the condition found, we believe, in *Homo Rhodesiensis*. It needs a somewhat less degree of prognathism of the incisor teeth, to produce the sharp margin found in Neanderthal man, resulting from the approximation of the paraseptal ridge to the lateral remnant of the crista prae nasalis.

We may mention here a further observation, namely that while usually the medial incisors have their long axes slightly divergent as they approach the nose, occasionally we find their axes directed somewhat medially. An example of the latter condition is R 25 (Aus. Mus.) and in this particular skull we find an unusual degree of prominence of the nasal spine and the paraseptal ridges.

We may finally observe that the crista may often be traced from the tip of the root of the median incisor to the lateral margin of the apertura. Moreover, it may be observed to be reinforced by the lateral incisor root and more laterally still by the canines.

On the basis of the above observations, we believe that a regular series of skulls may be traced from the anthropoid to the European, exhibiting a complete correlation between the above-mentioned factors and the shape of the lower margin of the apertura piriformis. First in the anthropoid skull, the incisor teeth are large, curved and prognathous, and relative to their size close up to the apertura of the nose. The anterior part of the palate is also flat. The set of their roots is also distinctly lateral. In these cases, the bone supporting the incisor teeth becomes rounded off at the apertura, curving laterally into a solid rounded pillar at the side of the apertura. This rounding of the bone at the side of the apertura is further correlated with the large canines, especially in the adult anthropoid. Meanwhile, the taking up of the thrust of these teeth, in part horizontally by the palate and in part laterally by the solid pillar of bone at the lateral margin of the apertura, obviates any need for the septum to play any very active part in the support of the teeth. Hence the nasal spine is small or absent.



Next we come to the similar type found in aboriginal skulls, which however differs in that the teeth are now reduced, less prognathous and probably their long axes less divergent. Nevertheless the teeth are still large, prognathous, curved and close up to the nose, while the palate is flattened, i.e., not arched. In these a nasal spine commences to develop to help in taking up the more vertical thrust of the incisors. Actually we find in these *orygmoeraspedote* aboriginal skulls, that the spine is never absent, though usually very poorly developed. Further, in these same skulls the canine teeth have undergone reduction and the lateral margin of the apertura is consequently much sharper than in the anthropoid, though frequently showing some degree of rounding off, especially at its base.

Turning to the next stage, we find that the teeth become less prognathous, less curved, but still remain close up to the nose, thus their thrust becomes still more vertical and consequently we get a strut of bone developing, viz., the *crista praenasalis*. Further the nasal spine becomes more projecting. The anterior part of the palate is still flattened. This gives us the *bothroeraspedote* skull with a *fossa praenasalis*. We may remark that in the *bothroeraspedote* skull, the *margo infranasalis* also becomes more defined, but while its paraseptal portion is probably related to tooth pressure, the anterior dental portion may or may not be.

The next in the series is the *amblycraspedote* type in which the teeth, though apparently of much the same size, become still less curved and less prognathous, while remaining close up to the nose. Hence their thrust is delivered still more vertically. In these skulls the *area praenasalis* becomes narrowed and partly thrust on to the face; the *crista praenasalis* and the *margo infranasalis* become approximated, the *crista* developing only laterally, while the paraseptal ridge become accentuated medially, with the narrow *area praenasalis* lying obliquely between them. At the same time, the nasal spine becomes more projecting, while the palate anteriorly now shows a modern degree of arching.

Finally, we come to the *oxycraspedote* condition, in which the teeth, whether large or small, are straight and disposed almost vertically, and may be close up to or distant from the nose. In these the *crista praenasalis* disappears medially, but its lateral portion fusing with the paraseptal ridge, forms a sharp margin separating nasal cavity from alveolar bone of the face, and the nasal spine is markedly projecting. It is probable that we may best interpret this condition as one in which the *praenasal area* has been thrust forward on to the face. At the same time the palate becomes well arched. The above theory gives a broad outline of what we consider to be the general trend of evolution of this region and assumes that the main factors concerned are the teeth (as regards size, curvature, and degree of alveolar prognathism, together with their distance from the nasal aperture). Deviations, when they occur, may be correlated with variations in the factors previously named, and of these two may be specially mentioned.

(a) The first case is that in which the tips of the incisor teeth are widely separated from the nose (1 cm. or more). In such cases, if the teeth are very large and markedly prognathous, the ordinary orygmocraspedote skull character may obtain (*Aus. Mus.* B 3715 and B 1178). The Talgai skull belongs to this group, as the incisor teeth were very large and markedly prognathous, and the distance of the central incisor root apices from the lower margin of the apertura piriformis is certainly not less than 1.0 cm. In other of these cases, we find the teeth are either smaller or the prognathism is slightly less marked. In these the teeth are so widely separated from the margo infranasalis, that there is a thick



Fig. 4. Photo of skull of African negro (A. D. No. 232). Oblique view to illustrate unusual type of Apertura piriformis, as regards its lower edge.

mass of bone supporting them before ever the nasal aperture is reached. At the same time the floor of the nose seems to be tilted backwards to such an extent that the alveolus, in spite of its prognathism, really meets the floor of the nose nearly at a right angle. Hence the medial portion of the crista prae-nasalis does not develop, and the result is a type somewhat resembling the oxycraspedote skull, with a blunt angulation of the edge of the apertura piriformis (fig. 4).

From the imperfect casts and data at our disposal it would seem that an accentuation of this condition is seen in *Homo Neanderthalensis* (Smith Woodward (17)).

(b) The second deviation is that mentioned by Klaatsch. In this case, the fossa praenasalis, instead of lying obliquely at a slope intermediate between that of the floor of the nasal cavity and the alveolar bone of the incisor teeth, has been so tilted upwards as to lie parallel with the floor of the nose and almost inside the nasal cavity; further the crista has been converted into the apparent margin of the apertura, but the margo infranasalis can be plainly seen inside the apertura, limiting posteriorly what is undoubtedly the fossa praenasalis. The fossa praenasalis therefore lies practically on the floor of the nasal cavity.

The probable explanation of this condition is that the teeth, while on the one hand disposed much more vertically than usual, nevertheless, lie considerably in advance of the nose, and hence the fossa praenasalis, instead of lying obliquely as in the ordinary *bothrocraspedote* skull, has been tilted up anteriorly, and so lies in line with the floor of the nasal cavity.

#### REMARKS UPON THE SHAPE OF THE SEPTAL CARTILAGE AND OF THE APERTURA PIRIFORMIS

In the previous section, we have outlined an hypothesis in which certain factors influence the bony area praenasalis. We believe that the same factors are probably active in moulding the shape of the septal cartilage and even of the apertura piriformis itself.

(a) *The septal cartilage.* Macalister realised this clearly when he stated that the projection of the nose and nasal septum, in the white races especially, is a negative feature, due to retraction of the incisors and canines, i.e., to orthognathism. Schultz<sup>(15)</sup> shows this in his fig. 4, p. 337.

We would suggest that, besides this passive factor in causing prominence of the nose in white races, there is a very active factor. If we examine the upward thrust of the incisor teeth in an orthognathic skull, it will be seen that this thrust, so far as it affects the septum, will tend to squeeze it out antero-posteriorly and thus tend still further to accentuate the tip of the nasal septum. At the same time the septum has probably more direct pressure to bear (at least anteriorly) in the orthognathic than in the prognathic skull (see figs. 5 and 6).

(b) These factors probably also mould the shape of the apertura piriformis to some extent. Schultz found that in the growth of the nose from infancy to adult life, the breadth of the bony apertura increases at a greater rate than the external nasal breadth, whereas the bony and external nasal height measurements showed the opposite relation, the bony apertura growing less in a vertical direction than the soft parts. These facts would receive a simple explanation on the hypothesis that the pressure of the incisor teeth influences the growth of the bony apertura, squeezing it more than the soft parts of the nose.



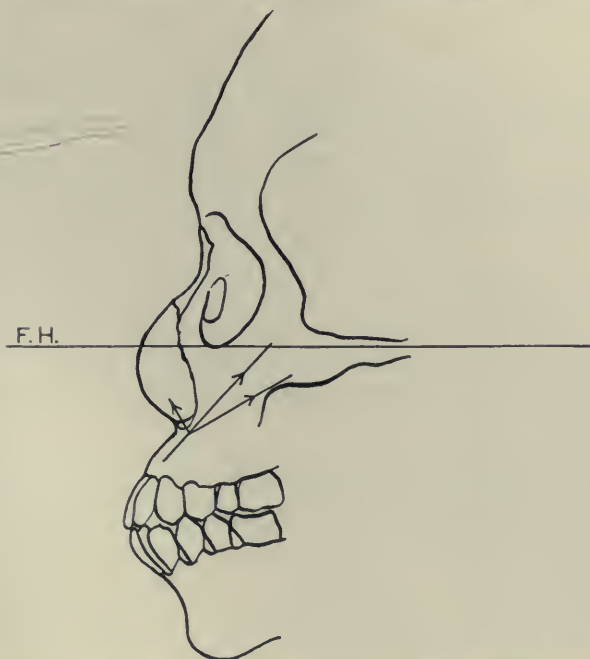


Fig. 5. Sketch suggesting the influence of the incisor teeth on the septum nasi in a prognathous Australian aboriginal.

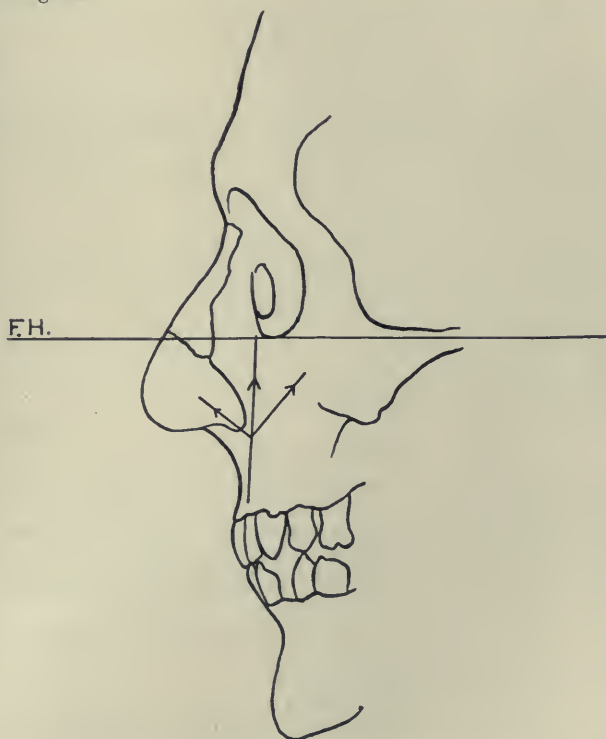


Fig. 6. Sketch suggesting the influence of the incisor teeth on the septum nasi in an orthognathous European.

## SUMMARY AND CONCLUSIONS

(1) The nose in the Australian aboriginal is very broad and flat, and its cartilages correspond very closely to those of the negro in shape.

(2) The ala nasi probably lies altogether lateral to the bony apertura.

(3) In the aboriginal the skull tends to be orygmocraspedote, and has well-developed praenasal areas, with the incisor teeth closely approximated to the nose.

(4) That in all skulls observed by us, whether of anthropoid apes, fossil type of man, of aboriginal, negroes, Melanesian or white type of man, the variations to be seen in the area praenasalis, and the lower margin of the apertura piriformis, are due chiefly to the tooth pressure of the upper incisor and canine teeth.

(5) That to estimate the tooth pressure, one must take into consideration both the force, the frequency and mode of application of the bite, and the size, curvature and age of the teeth, the direction of their axes and the approximation of their apices and the margin of the apertura piriformis.

In conclusion, we wish to thank Mr Louis Schaeffer, of the Anatomy Department, University of Sydney, for help in preparing the figures, and also the Director and officers of the Australian Museum, Sydney, for their help and courtesy; we also thank the Acting-Professor of Anatomy, Dr Maguire, for the use of laboratories and material.

## TABLE A

*Anthropometric Measurements of the Heads of two Australian Aborigines (with Definition of Terms and Table of Skin and Soft Tissue Thicknesses.)*

The terms and abbreviations used have been largely taken from Wilder (16).

In measuring skin and soft tissue thicknesses, a needle has been inserted as nearly as possible at right angles to the facial skin contour at the point measured.

We have retained the anthropometric abbreviations where measurements of skin thickness were made over corresponding points. The two heads are called H. B. 1 and D. B. 2. Of them H. B. 1 was injected with formalin (10 per cent.) and was slightly shrunken in the scalp region. D. B. 2 was prepared with the usual dissecting-room injection formula (glycerine, 12 parts, arsenic, 1 part, heat gently to boiling point. Take 1000 c.c. of the mixture, 1000 c.c. of carbolic acid, 1000 c.c. of methylated spirit, and 1000 c.c. of 20 per cent. formalin; well mixed and shaken) and was fairly normal.

## DEFINITION OF TERMS.

- |                   |   |
|-------------------|---|
| c.                | Commissural point. The point where a line joining the two medial palpebral commissures crosses the mid-line.  |
| cap.              | The most prominent point on the external angular process of the frontal bone.   |
| g <sup>1</sup> .  | A point 1 cm. lateral to the glabella in the same horizontal plane.   |
| go <sup>1</sup> . | A point at the lower and outer border of the mandible midway between the edges of the masseter.   |
| go <sup>2</sup> . | A point on the lower and outer border of the mandible immediately anterior to the masseter muscle.  |
| ii.               | The lowest point in the incisura intertragica.  |
| im.               | Malar point. The point of intersection of a vertical line through the ectoconchion (Wilder) and a horizontal line through the lowest point of the bony orbital margin. Roughly the most prominent point of the malar bone, but defined as above owing to the difficulty of determining the most prominent point in H. B. 1. |

<i>inf.</i>	Maximum depth of the infraorbital fossa between <i>ior.</i> and a horizontal line passing through the subnasale.
<i>ior.</i>	The centre point of the inferior orbital margin.
<i>la.</i>	The point where the lower edge of the ala nasi meets the skin of the upper lip.
<i>lcl.</i>	The lachrymal point. The point of junction of a horizontal line through <i>ior.</i> and the outer line or margin of the external nose.
<i>ms<sup>1</sup>.</i>	The most lateral point of the mastoid process.
<i>n<sup>1</sup>.</i>	Pseudonasion. The most depressed point in the nasal profile.
$\frac{n^1.-rh.}{2}$	The midpoint between the pseudonasion and the rhinion.
<i>nap.</i>	The greatest antero-posterior diameter of each anterior nasal aperture, i.e., the nostril length.
<i>nb.</i>	The lateral diameter of each nasal aperture, i.e., the nostril breadth.
<i>on.</i>	(See Wilder, p. 47.)
<i>on<sup>1</sup>.</i>	(See Wilder, p. 152.)
<i>p.</i>	The point where the sagittal plane intersects a line joining the centres of the two parietal eminences.
<i>pe.</i>	Parietal eminence.
<i>po<sup>1</sup>.</i>	The centre point of the external auditory meatus.
<i>pr<sup>1</sup>.</i>	The prosthion ( <i>pr<sup>1</sup>.</i> ) in the living is 1 mm. below the prosthion ( <i>pr.</i> ) on the skull.
<i>slm.</i>	The centre point in the sulcus mentolabialis.
<i>sn<sup>1</sup>.</i>	The centre point of the philtrum.
<i>sor.</i>	The centre point of each superior orbital margin; an antero-posterior measurement of thickness.
<i>sor<sup>1</sup>.</i>	The centre point of the lower border of each eyebrow, immediately below <i>sor.</i> ; an upward vertical measurement of thickness.
<i>tl.</i>	Temporal point. The centre point of a line joining the parietal eminence to the external angular process of the frontal bone.
$\frac{tr.-g.}{2}$	The midpoint between the trichion and the glabella.
<i>zy<sup>1</sup>.</i>	The base of the zygomatic arch near the ear just above the tragonion.
<i>zy<sup>2</sup>.</i>	The zygomatic tubercle.
<i>zyg.</i>	Zygomagonion. The thickness of the cheek at a point midway between the lower edge of the zygoma and the gonion in a line joining the zygomatic angle and the gonion. (The zygomatic angle is the angle between the frontosphenoidal and temporal processes of the zygoma.)
$\left. \begin{matrix} zyo^1. \\ zyo^2. \end{matrix} \right\}$	$\left. \begin{matrix} \text{Points just behind (} zyo^1. \text{) and in front of (} zyo^2. \text{) the naso-labial fold, on a line joining the} \\ \text{most projecting anterior inferior point of the zygoma with the angle of the mouth.} \end{matrix} \right\}$

# Anthropometric Measurements of two Australian Aboriginal Heads (known as H. B. 1 and D. B. 2).

				H. B. 1	D. B. 2
A. GENERAL:					
(1) Vertex-subnasale ... <i>v.-sn.</i>				17.23 cm.	19.75 cm.
(2) Trichion-pseudonasion ... <i>tr.-n<sup>1</sup>.</i>				Both somewhat bald	
B. CRANIUM:					
(1) Glabella-opisthocranion ... <i>g.-op.</i>				19.8 cm.	21.3 cm.
(2) Glabella-inion ... <i>g.-i.</i>				19.65	20.2
(3) Greatest breadth ... <i>eu.-eu.</i>				14.3	14.35
(4) Between the frontotemporalia ... <i>ft.-ft.</i>				10.7	10.85
(5) Bimastoid breadth ... <i>ms<sup>1</sup>.-ms<sup>1</sup>.</i>				12.65	13.85
(6) Tragonion-tragonion ... <i>t.-t.</i>				14.5	14.95
(7) Preaurale-preaurale ... <i>pra.-pra.</i>				14.0	14.35
(8) Trichion-pseudonasion ... <i>tr.-n<sup>1</sup>.</i>				—	—
(9) Tragonion-vertex ... <i>t.-v.</i>				11.80	15.8
(orthogonal projection)					
Auricular radiometer	(10) <i>po<sup>1</sup>.-vertex</i>	...	<i>po<sup>1</sup>.-v.</i>	11.8	13.75
	(11) <i>po<sup>1</sup>.-glabella</i>	...	<i>po<sup>1</sup>.-g.</i>	11.1	11.9
	(12) ...	...	<i>po<sup>1</sup>.-on<sup>1</sup>.</i>	11.15	12.1
	(13) Maximum frontal radius	...	...	11.25	11.98
	(14) ...	...	<i>po<sup>1</sup>.-op.</i>	11.6	11.7
	(15) <i>po<sup>1</sup>.-inion</i>	...	<i>po<sup>1</sup>.-i.</i>	9.5	9.15



(The above measurements (auricular radiometer) were really taken from a dioptographic tracing, which gave an exact orthogonal projection of the head, and *po*<sup>1</sup>. was taken at the centre of the meatus. Hence they are projection measurements.)

			H. B. 1	D. B. 2	
	(16) Maximum horizontal circumference		55.7 cm.	59.5	cm.
	(17) Longitudinal arc ... <i>n</i> <sup>1</sup> .- <i>i</i> .		33.8	38.0	
	(18) Transverse arc, trigion-trigion ... <i>t</i> .- <i>t</i> .		30.3	36.0	
C. THE FACE:					
	(1) Pseudonasion-stomion ... <i>n</i> <sup>1</sup> .- <i>sto</i> .		7.8	7.4	
	(1 <i>a</i> ) " prosthion ... <i>n</i> <sup>1</sup> .- <i>pr</i> <sup>1</sup> .		6.7	(no teeth)	
	(2) " gnathion ... <i>n</i> <sup>1</sup> .- <i>gn</i> .		12.6	11.5	
	(3) Stomion-gnathion ... <i>sto</i> .- <i>gn</i> .		5.0	4.6	
	(4) Trichion-gnathion ... <i>tr</i> .- <i>gn</i> .		—	—	
	(5) Zygon-zygon ... <i>zy</i> .- <i>zy</i> .		14.75	14.1	
	(6) Intermalar breadth ... <i>im</i> .- <i>im</i> .		12.9	12.7	
	(7) Ectocoenchion-ectocoenchion ... <i>ec</i> .- <i>ec</i> .		12.0	12.0	
	(8) Ectocanthion-ectocanthion ... <i>ex</i> .- <i>ex</i> .		10.2	9.2	
	(9) Endocanthion-endocanthion ... <i>en</i> .- <i>en</i> .		3.7	3.9	
	(10) Gonion-gonion ... <i>go</i> .- <i>go</i> .		13.35	11.0	
	(11) Pseudonasion-glabella ... <i>n</i> <sup>1</sup> .- <i>g</i> .		1.9	1.75	
	(12) Pseudonasion-commissural point ... <i>n</i> <sup>1</sup> .- <i>c</i> .		0.70	0.70	
	(13) Ectocanthion-ectocanthion (tape) 2 ( <i>n</i> <sup>1</sup> .- <i>ec</i> .)		14.8	14.0	
Auricular radiometer	(14) <i>po</i> <sup>1</sup> .-prosthion ... <i>po</i> <sup>1</sup> .- <i>pr</i> <sup>1</sup> .		11.3	—	
	(15) <i>po</i> <sup>1</sup> .-pogonion ... <i>po</i> <sup>1</sup> .- <i>pg</i> .		13.3	13.0	
D. THE NOSE:					
	(1) Pseudonasion-subnasale ... <i>n</i> <sup>1</sup> .- <i>sn</i> .		5.1	4.75	
	(2) Alare-alore ... <i>al</i> .- <i>al</i> .		5.0	5.7	
	(3) Pronasale-subnasale ... <i>prn</i> .- <i>sn</i> .		1.9	1.95	
	(4) Pseudonasion-pronasale ... <i>n</i> <sup>1</sup> .- <i>prn</i> .		4.25	4.3	
	(5) Pseudonasion- <i>la</i> . ... <i>n</i> <sup>1</sup> .- <i>la</i> .		5.61	5.13	
	(6) Nostril length ... <i>nap</i> .	R. 0.95	R. 1.0		
		L. 0.95	L. 1.1		
	(7) Nostril breadth ... <i>nb</i> .	R. 1.3	R. 2.25		
		L. 1.3	L. 1.85		
Auricular radiometer	(8) <i>po</i> <sup>1</sup> .-pseudonasion ... <i>po</i> <sup>1</sup> .- <i>n</i> <sup>1</sup> .		10.3	10.65	
	(9) <i>po</i> <sup>1</sup> .-rhinion ... <i>po</i> <sup>1</sup> .- <i>rh</i> .		10.7	10.8	
	(10) <i>po</i> <sup>1</sup> .-pronasale ... <i>po</i> <sup>1</sup> .- <i>prn</i> .		10.9	12.4	
E. THE MOUTH:					
	(1) Cheilion-cheilion ... <i>ch</i> .- <i>ch</i> .		6.75	6.00	
	(2) Subnasale-stomion ... <i>sn</i> .- <i>sto</i> .		3.25	2.95	
	(3) Stomion- <i>slm</i> . ... <i>sto</i> .- <i>slm</i> .		4.75	2.15	
	(4) Subnasale- <i>slm</i> . ... <i>sn</i> .- <i>slm</i> .		8.0	5.10	
	(5) Labrale superius-labrale inferius ... <i>ls</i> .- <i>li</i> .		2.65	1.80	
Auricular radiometer	(6) <i>po</i> <sup>1</sup> .-stomion ... <i>po</i> <sup>1</sup> .- <i>sto</i> .		12.4	12.7	
F. THE EAR:					
	(1) ... <i>obs</i> .- <i>obi</i> .	R. 5.1	R. 5.45		
		L. 5.1	L. 5.8		
	(2) ... <i>sba</i> .- <i>sa</i> .	R. 5.8	R. 7.45		
		L. 6.0	L. 7.45		
	(3) ... <i>pa</i> .- <i>pra</i> .	R. 3.6	R. 3.9		
		L. 3.6	L. 3.7		
	(4) ... <i>t</i> .- <i>tu</i> .	R. 3.3	R. 3.85		
		L. 3.1	L. 2.75		
	(5) ... <i>sa</i> .- <i>ii</i> .	R. 4.8	R. 5.30		
		L. 4.8	L. 5.30		
	(6) ... <i>ii</i> .- <i>sba</i> .	R. 1.95	R. 2.55		
		L. 2.3	L. 2.55		

Table of Thickness Measurements of Soft Parts.

		H. B. 1	D. B. 2
CRANIUM:	<i>op.</i>	0.40 cm.	0.80 cm.
	<i>p.</i>	0.60	0.90
	<i>pe.</i>	R. 0.45	R. 0.80
		L. 0.60	L. 0.80
	<i>tr.</i>	0.25?	0.40?
	$\frac{tr.-g.}{2}$	0.30	0.45
	<i>g.</i>	0.40	0.50
	<i>g</i> <sup>1</sup> .	R. 0.35	R. 0.45
		L. 0.4	L. 0.5
FACE:	<i>sor.</i>	R. 0.50	R. 0.65
		L. 0.55	L. 0.80
	<i>ior.</i>	R. 0.45	R. 0.50
		L. 0.3	L. 0.60
	<i>inf.</i>	R. 1.5	R. 2.0
		L. 1.7	L. 2.2
	<i>im.</i>	R. 0.90	R. 0.7
		L. 0.90	L. 0.7
	<i>zy.</i>	R. 0.90	R. 0.8
		L. 0.70	L. 0.7
	<i>zy</i> <sup>1</sup> .	R. 0.95	R. 1.2
		L. 0.95	L. 1.1
	<i>zy</i> <sup>2</sup> .	R. 0.50	R. 0.5
		L. 0.6	L. 0.5
	<i>tl.</i>	R. 1.05	R. 1.0
		L. 1.05	L. 1.05
	<i>zyg.</i>	R. 1.8	R. 1.7
		L. 2.2	L. 1.7
	<i>pg.</i>	1.05	1.00
	<i>gn.</i>	1.10	0.60
	<i>go</i> <sup>2</sup> .	R. 1.45	R. 1.10
		L. 1.30	L. 1.3
	<i>go</i> <sup>1</sup> .	R. 1.60	R. 1.70
		L. 1.40	L. 1.5
	<i>go.</i>	R. 1.80	R. 1.20
		L. 1.50	L. 1.5
	<i>zyo</i> <sup>1</sup> .	R. 2.15	R. 2.2
		L. 2.3	L. 2.0
	<i>zyo</i> <sup>2</sup> .	R. 1.7	R. —
		L. 1.5	L. —
NOSE:	<i>n</i> <sup>1</sup> .	0.4	0.75
	$\frac{n^1.-rh.}{2}$	0.3	0.55
	<i>rh.</i>	0.5	0.50
	<i>lcl.</i>	R. 0.8	R. 0.8
MOUTH:		L. 0.55	L. 1.0
	<i>sn.</i>	0.83	1.20
	<i>sn.</i>	0.80	1.20
	<i>sto.</i>	0.90	Edentulous
	<i>slm.</i>	1.10	1.20
	<i>ms.</i>	—	R. 1.50
		—	L. 1.20
	<i>ms</i> <sup>1</sup> .	—	R. 0.55
		—	L. 0.60
	<i>sor</i> <sup>1</sup> .	—	R. 1.0
		—	L. 1.0
	<i>eap.</i>	—	R. 0.2
		—	L. 0.3

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# ON THE DEVELOPMENT OF THE CRANIAL MUSCLES OF TATUSIA AND MANIS

By F. H. EDGEWORTH, M.D.

(The figures referred to in text will be found as Plates at end of Article)

## TATUSIA

OUR knowledge of the adult anatomy of the cranial muscles in Xenarthra and Manidae is now fairly extensive, though the part played by the cervical nerves in the innervation of the hypobranchial spinal muscles, of the Subcutaneus colli and of the Cucullaris groups is in many cases still obscure.

Windle and Parsons, in 1899, gave a summary of what was then ascertained, and since that date many papers have been published dealing with individual muscles or groups of muscles. On the other hand, save for a few observations I published in 1914 and 1916, no account has been given of the development of these muscles, and the following paper is a contribution to the subject based on a study of *Tatusia novemcincta* and *Manis javanica*.

Knowledge of the adult anatomy of the cranial muscles of Tatusia has grown in the following way. Macalister (1872) described the facial and auricular muscles, the Sterno-mandibularis, Sterno-hyoideus, Sterno-thyroideus, Trapezius, Sterno- and Cleido-mastoideus, and a monogastric Digastric muscle "attached to beneath the jaw." Chaîne (1900) described the Intermandibularis, Genio-hyoideus, and Genio-glossus; he did not mention the existence of any digastric muscle. Van Kampen (1905) mentioned the existence of a Stylo-mastoideus (here termed the "Interhyoideus dorsalis"). Lubosch (1908) described the Pterygo-tympanicus and the two Pterygoid muscles. Bijvoet (1908) identified the Digastric muscle of Macalister as a Mandibulo-auricularis, and stated that he could not find any Digastricus posterior or Stylo-hyoideus (his fig. No. 9, however, shows an unnamed muscle apparently identical with Toldt's Digastricus posterior). Toldt (1908) described a Digastricus posterior, taking origin from the temporal bone and passing down, band-like, to the lateral edge of the Sterno-mandibularis, where it was continued into an aponeurosis on the dorsal surface of that muscle, and was united to the posterior edge of the Intermandibularis. He also mentioned the existence of a Stylo-glossus. Fawcett (1921), in the course of his account of the development of the Chondrocranium, described the ocular muscles in the 12 mm. and the Stapedius in the 17 mm. embryo.

The embryological memoirs of Fernandez, Newman and Patterson, and Patterson, do not deal with the cranial muscles.

*Masticatory muscles.* In the 10 mm. embryo (figs. 1-4) the primordium of

the masticatory muscles is separated from the Intermandibularis and forms a mass above Meckel's cartilage. The muscles into which it develops are all formed and distinct but are not completely separated from one another. The upper end of the Temporalis is not attached to any skeletal structure; its inner surface is continuous with the Pterygoideus externus, and its lower end with the Masseter. The Pterygoideus externus passes backwards and outwards above Meckel's cartilage. The Pterygoideus internus passes backwards and downwards internal to Meckel's cartilage; its proximal end is continuous with the Pterygoideus externus and the Pterygo-tympanicus. The Pterygo-tympanicus passes backward for a short distance, but does not reach Meckel's cartilage. The Tensor tympani, the proximal end of which is continuous with that of the Pterygo-tympanicus, passes backwards and outwards towards the Malleus portion of Meckel's cartilage.

In the 12 mm. embryo (figs. 7-12) the muscles, with the exception of the Temporalis which is continuous with the Masseter, have become separated from one another. The Temporalis arises from the parietal plate, passes downwards and forks over the coronoid process of the primordium of the mandibula. The Masseter arises from the lower edge and inner surface of the primordium of the zygomatic arch, and passes down outside the primordium of the mandibula. The Pterygoideus externus is inserted into the condyloid process of the mandibula. The Pterygoideus internus is inserted into the inner surface of the mandibula below Meckel's cartilage.

Subsequent changes are as follows. In the 15, 17 and 20 mm. embryos (figs. 17-19) the proximal portion of the Tensor tympani has disappeared. The Pterygo-tympanicus takes origin just outside the primordium of the Pterygoid bone, below the Ala temporalis, and passes backwards towards the Malleus portion of Meckel's cartilage; it has no insertion into any skeletal element, the os tympanicus not being yet formed. From it arises the proximal end of the persisting distal portion of the Tensor tympani which passes backwards to the Malleus portion of Meckel's cartilage. In the 30 mm. embryo the Pterygoid bone had ossified, and the Pterygo-tympanicus takes origin from it; it passes backwards and forks, one limb is inserted into the tympanic bone, and the other is continuous by means of a fine tendon with the Tensor tympani, the origin of which, however, is mainly from the outer wall of the auditory capsule.

The Intermandibularis in the 10 mm. embryo (fig. 4) forms a transverse sheet between, but is not attached to, the two cartilages of Meckel. In the 12 mm. embryo (figs. 13 and 14) the posterior edge of the muscle diverges backward and is slightly concave, fitting up against the anterior surfaces of the salivary glands. In the 20 mm. embryo (fig. 28) the lateral edges of the muscle are attached to Meckel's cartilage.

There is no Digastricus anterior in the 10 mm. embryo. It is formed in the 12 mm. embryo (fig. 15)—apparently proliferated from the ventral surface of the Intermandibularis. It passes from the median raphe of the hinder part of

the Intermandibularis transversely outwards for a short distance, and has no lateral attachment. In the 20 mm. embryo (fig. 28) it has become oblique in position, passing forwards and outwards from the transverse aponeurosis of the Interhyoideus ventralis to the mandibula. In the 30 mm. embryo the attachments of the Digastricus anterior and Sterno-hyoideus superficialis to the transverse aponeurosis of the Interhyoideus ventralis are lost, and the two muscles form one continuous muscle-strip, the Sterno-mandibularis.

The hyoid muscle-plate in the 10 mm. embryo (figs. 1-4) is separated into the Stapedius and the Interhyoideus. The former lies in the fossa Stapedii and is inserted into the stapes. The Interhyoideus passes down close to the Hyale s. hyoid bar to a transverse aponeurosis just behind the posterior edge of the Intermandibularis. In the 12 mm. embryo (figs. 9-15) the Interhyoideus is partially separated into dorsal and ventral parts. The Interhyoideus has no upper attachment; it passes down postero-external to the Hyale and is partially inserted into it and is partially continuous with the Interhyoideus ventralis. The transverse aponeurosis of the latter is continuous anteriorly with a median raphé to which are attached the hinder fibres of the Intermandibularis and the inner ends of the Digastrici anteriores. In the embryo of 20 mm. the upper end of the Interhyoideus dorsalis has extended upwards to the outer surface of the auditory capsule.

*Facial muscles and Subcutaneous colli.* In the embryo of 10 mm. (fig. 4) the primordium of these muscles is visible as a collection of cells in front of and below the ear. It extends upwards a little in front of the ear. Behind the ear is the primordium of the Retrahens aurem. In the 12 mm. embryo (figs. 7, 8, 10, 12, 14,) the primordium has spread forwards to the angle of the mouth, and down the neck as the Platysma (using the nomenclature of Boas and Paulli). The Orbicularis oris is visible round the mouth (figs. 14, 15), and the primordium of the Mandibulo-auricularis just in front of the ear (figs. 7-8). The Retrahens aurem is partially separated into two muscles, and spreads outwards, fan-like, on the back of the Concha auris. In the embryo of 20 mm. (fig. 25) the Zygomaticus, Levator anguli oris, and the Orbicularis palpebrarum, have developed and the origin of the Mandibularis has extended downwards to the posterior edge of the primordium of the mandibula. The fibres of the Platysma can be traced from the surface of the Masseter to the shoulder girdle. In the adult (Macalister) they are attached to the lateral border of the dorsal shield.

The Branchio-hyoideus s. Subarcualis rectus i passes in the 10 and 12 mm. stages (figs. 3, 12) from the C. branchiale i forwards and inwards to the lower end of the C. hyale. In the 17 and 20 mm. stages—in which the C. hyale has begun to separate into parts—it is inserted into the Hypohyale. It is innervated by the ix.

The prehyoid hypobranchial spinal muscles, in the 12 mm. embryo (figs. 9-14) consist of Genio-hyoideus, Genio-glossus, Hyo-glossus, Stylo-glossus, Transversus linguae, Transversus hyoideus and Hyo-epiglotticus. The Genio-



hyoideus passes from the anterior end of Meckel's cartilage backwards to the basibranchiale and C. branchiale i. Its posterior part broadens, is concave dorsally in transverse section, and is ventral to the posterior part of the Hyoglossus. In an embryo of 30 mm. the muscle forks posteriorly, into outer and inner fasciuli—the outer of which is attached to the C. branchiale i and the inner to the basibranchiale.

The Genio-glossus is not well defined in the 10 and 12 mm. embryos; in those of 15, 17 and 20 mm. (fig. 28) it forms a sharply-limited bundle which passes backwards ventral to the Transversus linguæ. It does not reach the hyoid, nor spread upwards in the tongue.

The Hyo-glossus and Stylo-glossus are barely separable from each other in the 10 mm. embryo (figs. 2, 3), but are separate structures in the 12 mm. (figs. 9–12), and succeeding stages. The former arises from the basibranchiale and cornu branchiale i and passes forwards below the stylohyale into the tongue, just internal to the Stylo-glossus. The Stylo-glossus arises from the stylohyale and passes forwards and slightly inwards along the lateral border of the tongue; its anterior part separates into slender fasciuli.

The Transversus linguæ forms a well-defined stratum of transverse fibres, with a median raphé (figs. 9–12). The fibres do not reach the lateral surface of the tongue. The muscle extends the whole length of the tongue, nearly as far as the hyoid bar. Just behind it, and probably developed by separation from it, are the Transversus hyoideus and Hyo-epiglotticus (figs. 10–12), which appear to be parts of one muscle. They lie dorsal to the basibranchiale. The fibres of the Transversus hyoideus pass across the middle line from the ventral end of one C. hyale to that of the other; those of the Hyo-epiglotticus pass from the C. hyale, on each side, backwards and inwards for a little distance. In the 20 mm. stage (figs. 24, 26) the lateral ends of the Transversus hyoideus are attached to the Hypohyalia, and the fibres of the Hyo-epiglotticus reach the primordium of the epiglottic cartilage.

The Transversus hyoideus and Hyo-epiglotticus are innervated by a recurrent branch of the lingual portion of the *xiii*th nerve.

In the 10 mm. embryo (fig. 5) the Rectus cervicis forms a flat antero-posterior strip in the neck. The inner edge joins that of its fellow. It has no posterior attachment. The Sterno-hyoideus superficialis separates from the ventral surface of the Rectus cervicis at the level of the thyroid cartilage and is inserted into the transverse aponeurosis of the Interhyoidei. The rest of the Rectus cervicis is inserted into the C. branchiale i. In the 12 mm. embryo (figs. 15, 16) the Sterno-hyoideus superficialis is separated from the Rectus cervicis throughout its whole length. The remaining part of the muscle is imperfectly separated into a median and a lateral part. The former is the Sterno-hyoideus, which is inserted into the basibranchiale and branchiale i. The lateral part forms the Sterno-thyroideus and Thyro-hyoideus, which are partially continuous. The Thyro-hyoideus is inserted anteriorly into C. branchiale i. In the 17 mm. embryo the posterior ends of the Sterno-hyoideus

superficialis, Sterno-hyoideus, and Sterno-thyroideus are attached to the dorsal surface of the Sternum at the level of the 2nd ribs, the first-named a little anterior to the other two.

In the 30 mm. embryo the posterior end of the Digastricus anterior and the anterior end of the Sterno-hyoideus superficialis have lost their attachments to the transverse aponeuroses of the Interhyoidei ventrales, and the muscles form a continuous structure—the Sterno-mandibularis.

The Trapezius in the 10 mm. (figs. 1–4) and 12 mm. (figs. 8–16) embryos is a continuous structure which arises from the dorsal fascia over the occipital region, and the neck, and anterior thoracic region. The anterior fibres pass backwards and downwards, the posterior fibres downwards. They are inserted into the acromial process of the scapula. A fasciculus—an incomplete Cleido-occipitalis—diverges from the ventral edge of the Trapezius and is inserted into the Clavicle external to the Cleido-mastoideus (figs. 9–15). In the 20 mm. embryo the Trapezius is separated into anterior and posterior portions; the former is inserted into the acromial process and the fascia over the Deltoid, whilst the latter, consisting of vertical fibres, is inserted into the outer surface of the acromial process.

The Sterno-mastoideus and Cleido-mastoideus in the 10 mm. embryo (figs. 2–4) are, with the exception of their anterior ends, separate structures. In the 12 mm. embryo (figs. 8–16) this anterior end is attached to the external surface of the auditory capsule. The Sterno-mastoideus passes backwards between the medial ends of the two clavicles—the sternum not yet being formed—whilst the Cleido-mastoideus is attached to the clavicle. In the 17 mm. embryo the former is attached to the anterior surface of the sternum at the level of the 1st rib.

*Pharyngeal muscles.* In the 10 mm. embryo (figs. 1–4) the Stylo-pharyngeus and Constrictor pharyngis form a continuous sheet on the dorsi-lateral surface of the pharynx. It is continuous posteriorly with the Constrictor oesophagi, and is not yet attached to skeletal structures. There is a slight palato-pharyngeal fold of the pharyngeal wall in the hyoid segment. In the 12 mm. embryo (figs. 9–16) the Stylo-pharyngeus and Constrictor pharyngis are attached laterally to the C. hyale, C. branchiale i, thyroid and ericoid cartilages. The Palato-pharyngeus has developed on the inner side of the fore part of the muscle sheet. In the 20 mm. embryo (fig. 20) the palatal folds meet in the middle line and are continuous posteriorly with the palato-pharyngeal folds. The Palato-pharyngeus has extended forwards ventro-external to the pharyngeal end of the Eustachian tube. In the 30 mm. embryo (figs. 29–31) the Constrictor pharyngis and Stylo-pharyngeus sheet forms, posteriorly, a Constrictor muscle, the dorsal edge of which meets that of its fellow. Further forwards it forms a longitudinal muscle which, anteriorly, turns inwards in the soft palate. In the anterior part of the pharynx is a thin transverse muscle; its outer part is ventro-external to the pharyngeal end of the Eustachian tube, whilst its inner part curves forwards into the soft palate dorsal to the muscle-



sheet formed by the Stylo-pharyngeus and Constrictor pharyngis. It is probable that this is formed by a transformation of the anterior part of the Palato-pharyngeus, whilst the posterior part of the muscle disappears. Stages between the 20 and the 30 mm. embryos were not available for affording evidence of these changes.

The Crico-thyroideus, passing from the cricoid to the thyroid cartilage, is already developed in the 10 mm. embryo (fig. 16, from the 12 mm. embryo).

*Laryngeal muscles.* In the embryo of 10 mm. (fig. 4) the primordium of the laryngeal muscles is situated in the larynx, and is not as yet differentiated into the muscles eventually derived from it. In the embryo of 12 mm. (figs. 13-16) these consist of the following: (a) Dilatator laryngis s. Crico-arytenoideus posticus, which takes origin from the dorsal surface of the cricoid cartilage and lateral side of its median crista and passes forwards and outwards to the processus muscularis of the arytenoid cartilage; (b) Laryngeus dorsalis s. Interarytenoideus, which is very minute and lies on the dorsal side of the arytenoid cartilages; (c) Laryngeus ventralis, which has as yet no origin, its fibres passing upwards to the arytenoid cartilage. In the embryo of 20 mm. (figs. 21-27), the Interarytenoideus takes origin from the dorsi-lateral surface of the arytenoid cartilage and passes upwards and forwards to a median raphé which is continued forward from the interarytenoid bridge. The Laryngeus ventralis is separated into the Crico-arytenoideus lateralis and Thyro-arytenoideus. The former arises from the anterior edge of the lateral part of the cricoid cartilage and is inserted into the processus muscularis of the arytenoid cartilage. The Thyro-arytenoideus takes origin from the thyroid cartilage, and is partially separated into Thyro-arytenoideus superior and inferior.

#### MANIS

The cranial muscles of *Manis* have been described by a number of investigators. Macalister (1872) described the Platysma, Trapezius, Sterno-mastoideus, Sterno-glossus, the two orbicular muscles, and the Levator labii superioris; and mentioned a Cleido-mastoideus. Ehlers (1894) described the lingual musculature in *Manis macrura* and *M. tricuspis*. Kohlbrugge (1898) stated that there is no Sterno-hyoideus, Genio-hyoideus, Omo-hyoideus, Stylo-pharyngeus, Stylo-hyoideus, nor any muscle associated with the aural concha ("Ohrmuschel"). He described the Buccinator, Digastricus, Subcutaneus colli (with an innervation from cervical nerves, the viii<sup>th</sup> being distributed to the face only, the Sterno-thyroideus (innervation from Ni. Cervs. ii and iii), Thyro-hyoideus (innervation from xii), and muscles of the tongue. These he said, lie in a sheath in front of the trachea and extend to the xiphoid. The sheath consists of an outer mantle formed by the Intermandibularis (innervation by v) which is attached to the jaw and base of the skull; to it pass fasciculi attached to the hyoid; and an inner mantle extending into the thorax and probably derived from the Genio-glossus, as it is innervated by the xii. There is a special muscle (innervation not determined) for the salivary gland, which



springs from the angle of the jaw close to the insertion of the Digastricus. Eschweiler (1898-99) described the Stapedius, and a strong unnamed muscle passing to the pharynx and attached to the cartilage of the Eustachian tube, and stated that there is no Tensor tympani. Windle and Parsons (1899) described the Masseter and a Digastric muscle inserted to an area on the jaw midway between the angle and the symphysis. Toldt (1906) stated that there is an equivalent of a Digastricus anterior in the form of a "Hyo-mandibularis," but gave no description. Schulman (1906) described the Masseter, the Pterygo-tympanicus (under the name Pterygo-spinosus) and Tensor veli palatini. Lubosch (1908) described the Temporalis, and a Pterygoideus internus, and stated that there is no Pterygoideus externus. I have stated previously (1914) that there is no Digastricus anterior (this, however, is an error, *vide infra*), described the Interhyoideus, and identified the Digastricus of Kohlbrugge, and of Windle and Parsons, as a Mandibulo-auricularis. The memoirs on the development of Manis by Weber, and by van Oordt, do not deal with the cranial muscles.

*Eye muscles.* The primordia of the eye muscles in an embryo of 10 mm. (figs. 40-42) consist of three cell masses representing the premandibular somite, the Obliquus superior, and the Rectus externus. Each one consists of an aggregate of cells, with no trace of any epithelium. The premandibular somite is triangular in shape, with its base towards the eyeball, and its apex directed towards the hypophysis. In an embryo of 14 mm. the premandibular somite has separated into the Rectus superior, internus, and inferior, and the Obliquus inferior. The Obliquus superior gains an origin from the Ala orbitalis, and the Obliquus inferior one from the nasal capsule (fig. 59). The other muscles gain an attachment to a slight lateral process at the base of the Ala orbitalis.

*Masticatory muscles.* In the 10 mm. embryo (figs. 41-43) the primordium of the masticatory muscles is a continuous  $\cap$ -shaped structure, open posteriorly, and embracing the R. mandibularis v. It is partially separated into a lateral portion, into which passes the R. lateralis, and a medial portion. The lateral portion has a slight upward projection lateral to the R. mandibularis v, and a downward projection lateral to the faintly-marked-out primordium of Meckel's cartilage. In the 13 mm. embryo (fig. 45) the primordia of the Pterygoideus externus and Temporalis are distinguishable in the lateral portion of the mass. In the 14 mm. embryo (figs. 48, 50) separation into muscles has taken place. The lateral portion is separated into Temporalis, Pterygoideus externus, and Masseter. The two former have as yet no origins, the Masseter arises from the inner surface and lower margin of the zygomatic portion of the superior maxilla. The medial portion has separated into Pterygoideus internus, Pterygo-tympanicus, and Pterygo-hyoideus. Neither has attained an attachment of origin. The Pterygoideus internus passes internal to Meckel's cartilage towards the primordium of the mandibula. The Pterygo-hyoideus passes backwards, internal to the upper edge of the Intermandibularis posterior, towards, but

not yet reaching, the C. hyale. In the  $18\frac{1}{2}$  mm. embryo the Pterygoideus internus has disappeared, and the posterior end of the Pterygo-hyoideus reaches the C. hyale. In the 21 mm. embryo (figs. 59, 60) the inner portion of the Masseter has separated from the outer portion, and forms the Zygomatico-mandibularis, which arises from the inner surface of the zygomatic portion of the superior maxilla. It is still more oblique in position than the Masseter, which arises from the lower edge of the superior maxilla. The Pterygoideus externus arises from the Palate bone and is inserted into the condyloid process of the jaw. The Pterygo-tympanicus lies lateral to the ventral process of the base of the Ala temporalis; a process projects from its upper part towards the os tympanicum (the Pterygo-tympanicus proper) whilst its ventral end extends downwards, forwards and inwards, in front of the Pterygoid bone, into the soft palate (Tensor veli palatini).

*Intermandibularis.* In an embryo of 10 mm. (fig. 43) the Intermandibularis is not continuous with the primordium of the masticatory muscles, nor has it any attachment to Meckel's cartilage. It has spread backwards a little. In an embryo of 14 mm. (fig. 52, 53), it has spread still further back and has separated into anterior and posterior parts. The Intermandibularis anterior is attached to the primordium of the mandibula, but the Intermandibularis posterior has no dorsal attachment. Each meets its fellow in a ventral median raphé, ventral to the Sterno-glossi. The dorsal edge of the Intermandibularis posterior extends upwards, and in an embryo of  $21\frac{1}{2}$  mm. is attached to the Pterygoid bone.

The Digastricus anterior is not yet developed in an embryo of 10 mm. In one of 14 mm. (figs. 52, 53) it is formed, and is a longitudinal muscle on the outer side of the Intermandibularis anterior and posterior, and like them is innervated by the N. mandibularis v. It is attached anteriorly to the primordium of the mandibula, just in front of the anterior edge of the Intermandibularis anterior. Traced backwards, it is found partially to separate into two fasciculi, one of which is attached to the C. hyale and the other to the inner surface of the salivary gland.

*Hyoid muscles.* In an embryo of 10 mm. (figs. 40, 41, 43) the hyoid bar consists of a continuous precartilaginous Stapes, Interhyale, and C. hyale. There is no artery perforating the Stapes at this or any subsequent stage. There is no crista parotica, or laterohyale, or fossa stapedii. The hyoid muscle-plate has separated into a Stapedius and Interhyoideus. The former (fig. 41) has not yet attained an attachment of origin and lies on the outer side of the auditory capsule, internal to the fifth nerve; it is inserted into the Interhyale. In a 14 mm. embryo (figs. 46-52) the Interhyale has disappeared, and the Stapes is in contact with the Incus. The crista parotica and laterohyale have developed; the latter has no connection with the C. hyale. The Stapedius lies in the fossa stapedii, and is inserted into the Stapes. The Interhyoideus takes origin from the C. hyale, passes downwards and inwards and meets its fellow in a ventral raphé ventral to the Sternoglossi and posterior to the Intermandibularis posterior. In an embryo of  $18\frac{1}{2}$  mm. (figs. 55-58) the Interhyoideus



has spread backwards—as far as the anterior end of the sternum, and forms an outer ventro-lateral sheath for the Sterno-glossi. It maintains its origin from the C. hyale, and is innervated by the R. hyoideus VII.

*Facial muscles and Subcutaneus colli.* The primordium of these muscles is first visible in the 10 mm. embryo (fig. 43) as an aggregate of cells in the hyoid segment, just beneath the ectoderm, and with no relations to the Interhyoideus. In the 14 mm. embryo it has spread extensively on to the face, extending forwards over the Masseter, upwards in front of the ear and upwards behind the ear. In the neck the back-growth forms the Sphincter externus and the Platysma (fig. 50). The former is a thin sheath of transverse fibres in the lateral and ventral parts of the neck. The Platysma is a thin narrow band, which is continuous anteriorly with the Sphincter externus; it extends backwards and slightly inwards towards the manubrium sterni. There is no Sphincter internus. In the 18½ mm. embryo (figs. 55–59) the Orbicularis palpebrarum, Orbicularis oris, and Levator labii superioris, are formed from a still further forward growth of this muscle-sheet on to the face, the Mandibulo-auricularis arises from the upgrowth in front of the ear, and a small Retrahens aurem from that behind the ear.

*Hypobranchial spinal muscles.* In an 8.5 (A) mm. (figs. 33–36) embryo the primordium of the hypobranchial spinal muscles is a continuous cell-column extending from the mandibular segment backward in the neck to an antero-posterior level a little posterior to the 6th aortic arch. Its posterior part lies dorsi-lateral to the coelom, which at this stage extends as far forwards as the 3rd branchial segment. In a second 8.5 mm. embryo (B)—of the same size but more advanced in development—the coelom has retreated in the neck and its anterior limit is at the level of the limb-bud. The muscle-primordium has extended backward laterally to the coelom. In a 10 mm. embryo (figs. 43–44) the primordium has separated, at the level of the 1st branchial bar, into anterior and posterior portions.

In a 14 mm. embryo (figs. 52, 53) the posterior part or Rectus cervicis is separated into a lateral and a median portion. The lateral portion forms anteriorly the Thyro-hyoideus and posteriorly the Sterno-thyroideus. The Thyro-hyoideus extends from the thyroid cartilage to the C. branchiale i. The posterior end of the Sterno-thyroideus extends backward in the thorax. The median portion of the Rectus cervicis forms the Sterno-hyoideus; its anterior end is fused with the posterior end of the Hyo-glossus to form a Sterno-glossus, which extends from the anterior end of the tongue into the thorax. The prebranchial portion of the hypobranchial spinal muscles forms the Genio-hyoideus, Genio-glossus, and the Transversus linguae, in addition to the Hyo-glossus. The Genio-hyoideus is attached anteriorly to the primordium of the mandibula; it extends backward, joining its fellow, below the Sterno-glossi to a point a little posterior to the level of the Interhyoidei, but at this stage no further. The Genio-glossus is attached anteriorly to the primordium of the mandibula, and extends backwards, close to the middle line, as far as the level



of the hyoid bar. The Transversus linguae forms a transverse band of fibres, the median edge of which is inserted into the lingual raphé.

In an 18.5 mm. embryo (figs. 55–58) the Genio-hyoidei have extended back to the level of the anterior end of the sternum, and are partially separated into median and ventro-lateral portions, which form an inner ventral sheath of the Sterno-glossi. The Transversus linguae has extended back to the level of the cricoid cartilage forming a dorsal inner sheath for the Sterno-glossi. The posterior ends of the Sterno-glossi are attached to the bifid posterior end of the sternum, those of the Sterno-thyroidei to the dorsal surface of the sternum at the level of the attachment of the 7th ribs.

*Cucullaris*. (By this term I denote the common primordium of the Trapezius, Cephalo-humeralis, and Sterno-mastoideus). It is first visible in a 8.5 (A) mm. embryo (fig. 32). At this stage the 3rd and 4th gill-clefts are separated from the endoderm, but their outer ends are continuous with the ectoderm. The median end of the 4th cleft extends a little further forwards than that of the 3rd, and the posterior end of the 3rd extends further back than does that of the 4th. The 4th aortic arch, i.e. that of the 2nd branchial segment, which is well developed in a 6 mm. embryo, is now, for the most part, atrophied and its remains are visible between the 3rd and 4th gill-clefts. The Cucullaris, to which the xith nerve passes, is visible as an aggregate of cells, the ventral end of which is lateral to the small gap between the 3rd and 4th clefts, i.e. in the 2nd branchial segment. It extends forwards for the length of  $230\mu$ , but does not extend backwards into the 3rd branchial segment.

In the 10 mm. embryo (figs. 43, 44) the Cucullaris extends backwards in the neck, but does not reach the region of the fore-limb. The Sterno-mastoideus has separated off from its posterior part.

In the 14 mm. embryo the Sterno-mastoideus, which has no attachments, is a separate structure. The Occipito-humeralis diverges from the ventral edge of the Trapezius, and is inserted into the humerus by two fasciculi, the dorsal of which has an insertion in common with the Deltoid, and the lower is inserted just below the Pectoralis. The Trapezius has spread backwards, a little beyond the scapula.

In the 18 mm. embryo the anterior end of the Sterno-mastoideus is attached to the auditory capsule, and its posterior end to the side of the manubrium steni. The Trapezius is attached to the spine of the scapula.

The Pharyngeal muscles are not yet formed in a 8.5 mm. embryo. In one of 10 mm. (figs. 43, 44) they consist of a Stylo-pharyngeus in the region of the hyoid and 1st branchial bars, and of a Constrictor pharyngis in that of the thyroid cartilage. In an embryo of 14 mm. (figs. 47–49) the Constrictor pharyngis, which is continuous posteriorly with the Constrictor oesophagi, extends forwards to the naso-pharynx, overlapping the Stylo-pharyngeus. The Stylo-pharyngeus (fig. 49) is attached to the C. hyale, it passes inwards and then upwards, hooking round the ventral edge of the Constrictor pharyngis. The palato-pharyngeal fold is slightly developed. Dorsal to it, and internal to

the Constrictor pharyngis is the Palato-pharyngeus muscle (figs. 47, 48). In an embryo of 21.5 mm. the ventral edge of the Constrictor pharyngis is attached to the C. branchiale i, the thyroid ala, and the cricoid cartilage (figs. 61–63). The palato-pharyngeal fold is continuous anteriorly with the soft palate. The Palato-pharyngeus extends forward in the soft palate, and its anterior edge is attached to the Pterygoid bone (fig. 60).

*Laryngeal muscles.* In the 8.5 mm. (A) embryo (figs. 32–36) the 3rd and 4th gill-clefts are continuous with the ectoderm, but not with the endoderm. The postbranchial body is a thickening of the lateral margin of the pharyngeal epithelium. There is no 2nd branchial nerve between the 3rd and 4th gill-clefts, the 4th aortic arch is represented by remnants only. The superior laryngeal nerve is the 3rd branchial nerve, entering the laryngeal region between the level of the 4th gill-cleft and the post-branchial body. The Aditus laryngis is bounded by the Plicae laterales. The primordium of the laryngeal muscles is postbranchial in position, extending from  $90\mu$  behind to the level of the hinder margin of the postbranchial body; its hinder end is continuous with the primordium of the Constrictor oesophagi. The recurrent laryngeal nerve passes transversely inwards from the vagus, behind the 6th aortic arch, to the hind end of the primordium of the laryngeal muscles.

In the 8.5 mm. (B) embryo (figs. 37–39) the Plicae inferiores have developed and bound the Aditus laryngis, their anterior ends abut against but do not join the back of the epiglottis (fig. 47). The front end of the laryngeal muscle primordium is  $70\mu$  in front of the postbranchial body, i.e. in the 3rd branchial segment. The hind end of the primordium is separated from the Constrictor oesophagi.

In the 8.5 mm. (B) embryo (fig. 38) the primordium of the thyroid cartilage has appeared at the level of the superior laryngeal nerve, i.e. in the 3rd branchial segment. In the 10 mm. embryo (fig. 44) there is a continuous primordium of the arytenoid and cricoid cartilages. The primordium of the laryngeal muscles is wholly in front of the postbranchial body (which is still continuous with the pharyngeal endoderm) and so branchial in position. It is not separated into portions.

In the 14 mm. embryo (figs. 48, 49, 51) the primordia of the arytenoid cartilages have partially separated from that of the cricoid cartilage; they are connected by a transverse dorsal bridge. The primordium of the laryngeal muscles has separated into a Dilator laryngis (Crico-arytenoideus posticus), Laryngeus dorsalis (lateral half of the Interarytenoideus) and Laryngeus ventralis (Thyro-arytenoideus).

In the 18.5 mm. embryo (figs. 55–58) the Thyro-arytenoideus arises from the basithyroid and from its posterior projection, which is tied to the Cricoid of a ligament.

In the 21.5 mm. embryo (cp. figs. 56 and 61) the dorsal bridge connecting the arytenoid cartilages has disappeared. The Thyro-arytenoideus has partially separated into the Thyro-arytenoideus superior arising from the Basithyroid and the Thyro-arytenoideus inferior arising from its posterior median process.

## COMMENTS.

The above recorded investigations afford an explanation of some of the many problems presented by the adult anatomy of the cranial muscles of *Xenarthra* and *Manidae*.

The primordium of the masticatory muscles in *Tatusia* separates into *Temporalis*, *Masseter*, *Pterygoideus externus*, *Pterygoideus internus*, *Pterygo-tympanicus*, and *Tensor tympani*. In *Manis* it separates into *Temporalis*, embryonic *Masseter*, *Pterygoideus externus*, *Pterygoideus internus*, the primordium of the *Pterygo-tympanicus* and *Tensor veli palatini*, and the *Pterygo-hyoideus*.

In *Tatusia* no *Zygomatico-mandibularis* is separated from the *Masseter*, which arises from the lower edge and ventro-medial surface of the zygomatic arch. A *Zygomatico-mandibularis* is not invariably present in *Xenarthra*. It is absent in *Tamandua* and *Myrmecophaga*, whilst it is formed in *Bradypus*, *Choloepus*, *Dasybus*, and *Tolypeutes*. In *Manis* the *Masseter* of earlier stages separates into the *Zygomatico-mandibularis* arising from the inner surface, and the *Masseter* arising from the lower edge of the superior maxilla.

The appearances in the 10 mm. stage of *Tatusia*, and the 13 mm. stage of *Manis*, show that *Pterygoideus externus* in its earliest stage is as closely associated with the *Pterygoideus internus* as with the *Temporalis*, but this is probably a secondary phenomenon related to its development during intra-uterine life, for in *Dasyurus*, where the *Pterygoideus externus* is formed after birth, it is developed from the primordium of the *Temporalis* and *Masseter* and has no relations with the *Pterygoideus internus*. This agrees with the innervation—for the *Temporalis*, *Masseter*, *Zygomatico-mandibularis*, and the *Pterygoideus externus* are innervated from the R. lateralis of the R. mandibularis v.

The *Pterygoideus externus* is present in all *Xenarthra*, arising by a single head in *Bradypus* and *Chlamyphorus*, by two heads in *Tatusia*, *Tamandua*, and *Dasybus*.

The *Pterygoideus externus* of *Manis* was considered by Lubosch to be a *Pterygoideus internus*—but in the embryo it arises from the palate bone (as in the adult) and passes backwards and outwards to the jaw dorsal to Meckel's cartilage—a course which shows that the muscle is a *Pterygoideus externus*. Further, it is innervated from the R. lateralis of the R. mandibularis v. The *Pterygoideus internus* of *Manis* atrophies—during its existence it passes characteristically downwards towards the primordium of the jaw internal to Meckel's cartilage. The muscle next behind the *Pterygoideus internus* forms in *Tatusia* the *Pterygo-tympanicus*, in *Manis* it forms both a *Pterygo-tympanicus* and a *Tensor veli palatini*, which remain in continuity even in the adult (Schulman). This formation of both muscles from the same primordium is not peculiar to *Manis*, for it also occurs in *Dasybus sexcinctus* (*Kostanecki*) and in *Bradypus marmoratus*.



The existence of the Pterygo-tympanicus in Xenarthra and Manidae is probably a primitive Mammalian feature, for the muscle is present in Ornithorhynchus. It does not occur in Marsupials, where the homologous primordium forms the Tensor veli palatini only, nor in any other Mammalian group—as far as is known.

In Tatusia there is a normal Tensor tympani. In later developmental stages the proximal portion disappears, and the proximal end of the persisting distal portion becomes attached to the Pterygo-tympanicus and the wall of the auditory capsule. This is similar to the occurrences in Dasyurus and the rabbit.

Eschweiler stated that there is no Tensor tympani in Manis, and study of these embryos confirms the statement. There is, however, a Pterygo-hyoideus muscle, which is innervated by the R. medialis of the R. mandibularis v. In the 14 mm. stage its primordium lies immediately behind that of the Pterygo-tympanicus and Tensor veli palati, in a position which agrees with that of the Tensor tympani of Tatusia. This, and the innervation, show that it is the homologue of the Tensor tympani of other Mammals.

Lubosch, from a study of the adult condition of the Pterygoid bone in Xenarthra and Manidae, was led to the opinion that in Bradypus, Choloepus, Myrmecophaga, Tatusia, Priodontes, Xenurus, and Manis, it is formed by a fusion of a Parasphenoid and a Parabasale. The theory, however, can be rejected for Tatusia and Manis, as in these animals the bone is formed from one centre only, behind that of the Palate bone.

Schulman and Toldt were of opinion that the Detrahens mandibulae of Monotremes is a muscle which is not present in any other Mammalian order.

It has not been found in Marsupials, nor is it developed in Tatusia or Manis. It is possible, however, that it exists in some Xenarthra, for Lubosch described a muscle in Tamandua, Dasypus, and Tolypeutes, under the title "Accessory head of the Masseter," which arises from the Tympanicum and passes downwards behind the Masseter to the angle of the jaw. It is innervated in Tamandua and Dasypus by a branch of the N. auriculo-temporalis v.

The innervation—determined by Lubosch—excludes the possibility that the muscle is a Mandibulo-auricularis, whereas this and the situation of the muscle suggest that it is homologous with the Detrahens mandibulae of Monotremes.

There is no record of any similar muscle in Choloepus by Mackintosh, nor in Myrmecophaga by Owen or Pouchet. The muscle in Bradypus called "Digastric" by Windle and Parsons, and the (variable) muscle in Chlamyphorus called "Digastric" by Macalister may be either homologous structures or instances of a Mandibulo-auricularis, for the innervation is not yet known.

*Stapedius.* In the 10 mm. stage of Manis the Stapedius is situated external to the auditory capsule, and is inserted into the Interhyale. Subsequently, on development of the crista parotica and fossa stapedii and disappearance of the Interhyale, the origin of the muscle shifts to the floor of the fossa stapedii and the insertion to the stapes. The corresponding early stages of Tatusia were not available.

These phenomena are in harmony with those previously published which show that the Stapedius was originally a Levator hyoidei—a condition which is the permanent one in Monotremes.

The upper end of the Interhyoideus in the embryos of *Tatusia novemcincta* I examined extended upwards to the mastoid process and the muscle became divided into dorsal and ventral portions, the former inserted into and the latter arising from, the C. hyale. The same arrangement must have occurred in the adult specimen examined by van Kampen (who, however, described only the upper part—under the name Stylo-mastoideus). On the other hand, the Interhyoideus was described by Chaîne and by Toldt as a single muscle arising from the mastoid process. This variation is not surprising, seeing how close the muscle is to the C. hyale. A similar variation occurs in *Choloepus*.

The varieties in the form of the Interhyoideus among *Xenarthra* are as follows. It is single and arises from the C. hyale in *Chlamydophorus* and *Tolypeutes*; single and arises from the C. hyale and Mastoid in *Dasypus villosus*; single and arises from the Mastoid in *Bradypus tridactylus*. It is separated into upper and lower portions in *Bradypus marmoratus*, *Myrmecophaga*, and *Tamandua*. It arises from the Mastoid and is either single or separated into upper and lower portions in *Choloepus* and *Tatusia*.

These variations suggest that *Xenarthra* are descended from forms possessing a digastric muscle, the posterior belly of which, i.e. the Interhyoideus, arose from the C. hyale. The other conditions present result from upgrowth of the dorsal end of the muscle and, in some species, its division into dorsal and ventral portions—the Interhyoideus dorsalis and ventralis.

The anterior element of the Sterno-mandibularis is—as was pointed out by Toldt—the representative of the Digastricus anterior. Its development in *Tatusia* shows that it is at first a transverse muscle which subsequently rotates into a longitudinal position with its original inner end posterior. This negatives Toldt's theory that the muscle is primarily longitudinal, a theory which fails to account for the transverse position of the muscle in Monotremes—a position it has from the first stage of its development—and also fails to account for the rotation of the muscle from a transverse to a longitudinal position in successive stages of development in *Dasypus*. In fact all the known developmental phenomena go to show the truth of Schulman's theory that the muscle when first developed consisted, like its "Muttermuskel," the Intermandibularis, of transverse fibres.

The transverse aponeurosis of the Interhyoideus, or Interhyoideus ventralis, is identical with, or forms a part of, the tendinous intersection in the Sterno-mandibularis in *Bradypus*, *Choloepus*, and *Tolypeutes*; whilst it passes dorsally to the Sterno-mandibularis in *Myrmecophaga*, *Tamandua*, *Dasypus*, and *Tatusia*. The above described developmental changes in *Tatusia* show that the condition of a continuous Sterno-mandibularis is secondary to one with an intersection. The non-attachment of the Interhyoideus or Interhyoideus ventralis to the Digastricus anterior in *Myrmecophaga*, *Tamandua*, *Dasypus*,



and *Tatusia*, is thus secondary only—it is not a primitive feature as is the case in *Monotremes*.

The posterior part of the Sterno-mandibularis s. Sterno-hyoideus superficialis is either a medial strip of the Sterno-hyoideus (*Bradypus*), or a superficial strip of either this muscle (*Dasypus*, *Tatusia*, *Tolypeutes*, *Chlamyphorus*), or of the Sterno-glossus (*Myrmecophaga*), or of the Sterno-genioideus (*Tamandua*). In the two last named animals there is no Sterno-hyoideus, so it is probable that this is represented by the posterior constituent of these muscles. The posterior part of the Sterno-mandibularis is thus not homologous with the whole of a Sterno-hyoideus in any instance.

The first steps in the formation of a Sterno-mandibularis in *Xenarthra* would thus appear to have been the separation of a Sterno-hyoideus superficialis from the Sterno-hyoideus, and the fixation of its anterior end to the transverse aponeurosis of an Interhyoideus.

In *Dasypus*, according to Toldt, the anterior portion of the Sterno-mandibularis is innervated by the vth, and the posterior portion by the xii<sup>th</sup> and N. Cerv. ii. In a 20 mm. embryo of *Tatusia* the anterior portion is innervated by the vth, and the posterior by the R. descendens xii. The xii before giving off this R. descendens is joined by a branch from N. Cerv. i. In *Tamandua*, according to Toldt, the whole of the Sterno-mandibularis is innervated by the vth. This seems a remarkable statement and needs verification. The innervation of the muscle is not known in other *Xenarthra*.

A Digastricus anterior is present in *Manis*. It is not yet developed in the 10 mm. embryo, and in the 13 and 14 mm. embryos forms a longitudinal muscle just external to the Intermandibularis. It arises from the primordium of the mandibula in front of the anterior edge of the Intermandibularis anterior, at about the junction of the anterior and middle thirds of Meckel's cartilage. It passes backwards and is partially separated into two fasciculi, one of which is attached to the C. hyale and the other to the inner surface of the salivary gland. It is innervated by the N. mandibularis v. Embryos of intermediate sizes were not available, so that the early stages in the development of the muscle could not be determined, but its relations to the Intermandibularis and its innervation show that the muscle is a Digastricus anterior.

The transformation of the Tensor tympani and Digastricus anterior into protractors of the hyoid bar is perhaps related to the non-development of any attachment of the Genio-hyoideus to it.

In *Manis javanica* the Interhyoideus arises from the C. hyale. In the 14 mm. embryo the muscle forms a vertical band, with a ventral median raphé, just behind the Intermandibularis. In later stages the ventral part of the muscle spreads backwards—in a 21 mm. embryo as far as the anterior end of the sternum—forming the posterior part of the outer sheath of the Sterno-glossi, the anterior part being formed by the Intermandibularis.

The Interhyoideus of *Tatusia* and *Manis javanica* is innervated by the R. hyoideus vii.



Ehlers described, in *Manis tricuspis* and *macrura*, a Glosso-vaginalis superficialis, spreading from the jaws down the whole length of the Sterno-glossi. There was also a portion of this Glosso-vaginalis superficialis which arose from the bulla tympanica and passed ventrally, superficial to the main sheet. The condition of the specimens did not allow of dissection of the nerves. Ehlers identified the main sheet with a Mylohyoid, i.e. an Intermandibularis and the superficial vertical strip with a Stylo-hyoideus.

Investigation of the nerve supply in better specimens would show whether the condition is as he stated, or whether—as is more probable—it is similar to that of an adult *Manis javanica*. The figure given by Ehlers admits of either interpretation. In either case the condition shows that the origin of the Inter-hyoideus may in Manidae spread up to the skull, just as in Xenarthra.

The lingual musculature in *Manis javanica* is formed by the Hyo-glossus, Sterno-hyoideus, Genio-glossus, Transversus linguae. A Stylo-glossus is not developed—an occurrence which suggests that the muscle here called Hyo-glossus is homologous with the primordium of the Hyo-glossus and Stylo-glossus of Tatusia, and not merely with the former muscle. The Genio-glossus<sup>1</sup> is similar to that of Tatusia. The Hyo-glossus and Sterno-hyoideus fuse and form a continuous Sterno-glossus, the hind end of which is attached to the bifid end of the sternum. The tongue has an outer and an inner sheath. The former is formed by the Intermandibularis and Interhyoideus. The Genio-hyoideus joins its fellow and grows backwards, as a ventral median and two ventro-lateral bands<sup>2</sup>, forming a ventro-lateral inner sheath to the Sterno-glossi. The Transversus linguae extends backwards as far as the ericoid and forms, in part, an inner dorsal sheath of the Sterno-glossi. The Hyo-glossus, Genio-hyoideus, and Sterno-hyoideus, do not gain any temporary attachment to the Hyo-branchial skeleton. In both Tatusia and Manis there are Thyro-hyoideus and Sterno-thyroideus, muscles. Their adjacent ends, which are partially continuous, are attached to the thyroid cartilage. In Manis the hind end of the Sterno-thyroideus, like that of the Sterno-glossus, grows backwards in the thorax.

In the 20 mm. stage of Tatusia the Thyro-hyoideus, Sterno-thyroideus, and Sterno-hyoideus, are innervated by the R. descendens XII, and the pre-hyoid hypobranchial spinal muscles by the lingual division of the nerve. In Manis, according to Kohlbrugge, the lingual musculature is innervated by two branches of the XII. The Genio-glossus, Transversus linguae, Genio-hyoideus are innervated by the anterior branch, and the Sterno-hyoideus constituent of the Sterno-glossus by the posterior branch (which might be called the R. descendens XII). The Thyro-hyoideus is innervated by a branch of the anterior division. The Sterno-thyroideus is innervated by the Ni. Cervs. ii and iii and not by the XII.

*Facial muscles and Subcutaneous colli.* In Manis the primordium of the

<sup>1</sup> Glossovaginalis profundis, stratum internum, of Ehlers.

<sup>2</sup> Glossovaginalis profundus, stratum medium and stratum externum, of Ehlers.

facial muscles and Subcutaneus colli develops in the hyoid segment and spreads forwards and upwards in front of the ear and backwards in the neck. In *Tatusia* the earliest stage was not available—in the 10 mm. stage the primordium had spread back into the 1st branchial segment. These phenomena are similar to those already described in *Dasyurus* and the pig. The upward growth in front of the ear forms the Mandibulo-auricularis in both animals.

Bijvoet found that in *Tatusia* the branch of the vii<sup>th</sup> to the Mandibulo-auricularis passes upwards in front of the ear. The same course was followed in the embryos of *Manis* examined as well as in *Tatusia*. This is what might be expected from the developmental phenomena. On the other hand Schulman found in many Mammals, including *Myrmecophaga*, that the branch of the vii<sup>th</sup> to the muscle passes round the back of the ear and forwards above it. He concluded that the "Mandibulo-auricularis trotz seiner vorgeschobenen Lage morphologisch mit den postauricularen Facialisgebiet zusammenhängt." But this conclusion does not hold for *Tatusia* and *Manis*.

The Mandibulo-auricularis has been recorded as present in *Choloepus*, *Myrmecophaga*, *Tamandua*, and *Dasypus*. It has not been recorded in *Bradypus*, *Tolypeutes* and *Chlamydomorphus*.

The Subcutaneus colli is very different in the two animals. In *Tatusia* there is a wide *Platysma*, but neither *Sphincter externus* nor *internus* exists. In *Manis* it consists of a *Sphincter externus* and a narrow band like *Platysma*, but there is no *Sphincter internus*.

In a 20 mm. embryo of *Tatusia* the facial and auricular muscles are innervated by the vii<sup>th</sup>. The Subcutaneus colli is innervated by the R. colli vii and Ni. Cervs. ii and iii. In *Manis javanica*, according to Kohlbrugge, the facial musculature is innervated by the vii<sup>th</sup>, and the Subcutaneus colli solely by cervical nerves, there being no R. colli vii. Kohlbrugge, who did not know the development of the muscles, was of opinion, on comparing the innervation of the Subcutaneus colli of *Man* and *Manis*, that either the R. colli vii of *Man* reaches the neck owing to disappearance of a cervical musculature, or that in *Manis* the territory which once belonged to *Facialis* musculature is taken over by spinal muscles and nerves. The latter theory, he said, is probably the true one. The developmental phenomena, however, in *Tatusia* and *Manis* show that in both animals the Subcutaneus colli is due to a backward spread from the hyoid segment. In the case of *Tatusia* there is thus a partial, in the case of *Manis* a total, replacement of vii<sup>th</sup> nerve innervation of the Subcutaneus colli by nerve fibres of the cervical segments into which growth takes place.

The hyo-branchial skeletal structures of *Manis* and *Tatusia* consist of a basibranchiale with cornua hyalia and branchialia i. In *Manis* the ventral end of the C. hyale joins the C. branchiale i, and the ventral end of the latter the Basibranchiale, the structures forming a continuous whole. In *Tatusia* (*vide* Fawcett) the C. hyale separates into parts, and its ventral end articulates with the basibranchiale. The structures are thus simpler in *Manis* than in *Tatusia*.



The 1st branchial muscle-plate of *Manis* atrophies, and no Branchio-hyoideus muscle is formed. In *Tatusia* this muscle is developed, and is innervated by the ixth.

The Transversus hyoideus and Hyo-epiglotticus are developed in *Tatusia*, as parts of one muscle, and probably by separation of the posterior edge of the Transversus linguae. They are not developed in *Manis*. The Hyo-epiglotticus has been recorded as present in *Myrmecophaga* (Owen, Pouchet), and in *Tamandua* (Bender). In the latter it is stated to have "the same innervation as the ventral longitudinal muscles." In many Ungulata both Transversus hyoideus and Hyo-epiglotticus exist as separate muscles. In the pig they are developed from the Transversus linguae and, as in *Tatusia*, are innervated by a recurrent branch of the lingual portion of the xii.

The origin of the Cucullaris could not be observed in *Tatusia*. The significance of the phenomena in *Manis* is doubtful. They possibly indicate that it is developed from a 2nd branchial muscle-plate. But the development is not known in Monotremes, Marsupials, and Xenarthra. In the pig and in *Erinaceus* it is developed from the 1st branchial muscle-plate.

Both Sterno-mastoideus and Cleido-mastoideus are developed in *Tatusia*; but only the first-named in *Manis*, which has no clavicle. This feature is not peculiar to *Manis*, for in *Bradypus*, *Myrmecophaga*, and *Tamandua*, where the clavicle is rudimentary, there is no Cleido-mastoideus.

A Cleido-occipitalis is present in *Chlamydophorus* as a separate muscle. In *Tatusia* and *Myrmecophaga* a homologous muscle diverges from the cervical portion of the Trapezius and is inserted into the clavicle. The Occipito-humeralis of *Manis* is probably a homologous muscle. The method of insertion into the humerus is not uniform in *Manidae*, for Macalister stated that in *Pholidotus indicus* and *Manis multiscutatus* there is an intersection between it and the Deltoid.

The division of the Trapezius of *Tatusia* into anterior and posterior parts is not constant in *Xenarthra*, for in *Myrmecophaga* and *Tamandua* the muscle forms a continuous sheet.

In a 20 mm. embryo of *Tatusia* the Cucullaris group is innervated by the xith, which receives a branch from N. Cerv. ii. In *Manis* (Kohlbrugge) the Trapezius is innervated by the xith which receives a branch from N. Cerv. ii, and also by branches from N. Cervs. iii, iv, and v passing directly to the muscle; the Sterno-mastoideus is innervated by the xi and N. Cerv. ii. This additional innervation by branches of cervical nerves—more marked in *Manis* than in *Tatusia*—is in relation to the spread of the Cucullaris into cervical segments. There is a similar additional cervical innervation in the case of the Rectus cervicis of *Tatusia*, and it is the sole one in the case of the Sterno-thyroideus of *Manis* (*vide supra*).

The pharyngeal muscles in both *Tatusia* and *Manis* consist of a Stylo-pharyngeus, Constrictor pharyngis, and Palato-pharyngeus. In *Tatusia* the Stylo-pharyngeus and Constrictor pharyngis form one muscle, which consists



posteriorly of constrictor fibres, and anteriorly of longitudinal fibres passing into the soft palate. In *Manis* the Stylo-pharyngeus passes towards the wall of the pharynx, ventral to the lower edge of the Constrictor pharyngis.

The Palato-pharyngeus is developed on the inner side of the Stylo-pharyngeus and Constrictor pharyngis, and forms a longitudinal muscle. This is preserved in *Manis*, whilst in *Tatusia*, apparently, the posterior part of the muscle disappears and the anterior part forms a curved transverse muscle, passing from the wall of the Eustachian tube to the soft palate.

The Epiglottic cartilage in *Tatusia* is developed in the epiglottis as a posteriorly concave structure, the ventral edges of which are attached to the dorsal edge of the thyroid cartilage (figs. 29, 30). The epiglottic cartilage in *Manis* is similar in shape, but differs in that its ventral edge is attached to the Basithyroid (fig. 54). But this condition is not constant in *Manidae*, for Albrecht stated that in *Manis gigantea* its lower edge is attached to the upper edge of the thyroid cartilage.

Investigation of the first stage of *Manis* (fig. 34) shows that the Aditus laryngis is bounded by the Plicae laterales<sup>1</sup>. In the next stage (fig. 37) the Plicae inferiores<sup>2</sup> have developed, and bound the Aditus. Their anterior ends are close to, but do not join, the back of the epiglottis. Finally, the Plicae laterales overtop the Plicae inferiores, the position of which is now relatively more ventral. The changes in *Tatusia* are similar (figs. 30, 31), but the first stage had been passed in the 10 mm. embryo.

In this respect *Manis* and *Tatusia* resemble the pig and rabbit, and differ from *Dasyurus*, in which the Plicae inferiores have their permanent position from the time of their first development. The difference is perhaps, as previously suggested, related to the shorter period of intra-uterine life in *Dasyurus*.

The Plicae inferiores do not fuse with the epiglottis and hence do not become secondary ary-epiglottic folds. In this respect *Manis* and *Tatusia* resemble *Dasyurus* and differ from the pig and rabbit in whom fusion occurs. The condition in adult *Xenarthra* is variable, e.g. in *Tamandua didactyla* the Plicae inferiores fuse with the epiglottis (Göppert), whilst in *Tamandua tetractyla* they do not (Bender).

In *Manis* determination of the segment of origin of the thyroid cartilage is possible. The superior laryngeal nerve passes into the larynx posterior to the 4th gill-cleft, between that and the postbranchial body, i.e. in the 3rd branchial segment. The thyroid cartilage is developed subsequently and at the same antero-posterior level, and is consequently a 3rd branchial structure. It is not added to by any skeletal structure in front.

The corresponding early stages of *Tatusia* were not available.

In *Manis* there is only one superior laryngeal nerve. In *Tatusia* the nerve enters the larynx by two branches (figs. 13, 23, 24)—an anterior and a posterior.

<sup>1</sup> Plicae laterales (Symington), Partes laterales epiglotticae (Göppert).

<sup>2</sup> Plicae inferiores (Albrecht), Plicae ary-epiglotticae (Göppert).

The latter, in the 20 mm. stage, enters above the superior border just in front of the junction of the C. branchiale i with the thyroid cartilage—in the same position as the single nerve in *Manis*. It is therefore possible that in *Tatusia* there are 2nd and 3rd branchial nerves, but investigation of earlier stages is necessary to determine the matter. It may be added that this entry of the superior laryngeal nerve by two branches is not peculiar to *Tatusia*; it also occurs in *Bradypus* and *Myrmecophaga* (Dubois).

In regard to these questions it is interesting to recall the statement of Dubois, made in 1886. "The N. laryngeus superior represents the 3rd branchial nerve," and "it must remain an open question whether the 2nd branchial nerve has disappeared or whether it is fused with the N. laryngeus superior, and that its anterior branch so frequently present in Marsupials and Placentalia represents it."

It follows from the above that the thyroid cartilage of *Tatusia* may turn out to be either a 2nd branchial skeletal structure, as suggested by Fawcett, or a 3rd branchial structure, as in *Manis*; or the result of fusion of 2nd and 3rd branchial structures, as in *Trichosurus*.

The N. laryngeus recurrens passes into the larynx dorsal to the cricothyroid articulation in both *Tatusia* and *Manis*, and also in *Tamandua* (Bender). In this relationship these animals agree with other Eutheria, and differ from Monotremes and Marsupials in which the nerve passes forward ventral to the articulation.

The cricoid and arytenoid cartilages in *Tatusia* and *Manis* are formed as a continuous whole. On separation, the arytenoid cartilages are found to be connected by a dorsal bridge. This interarytenoid bridge does not persist in either animal, e.g. in *Tatusia* it is present up to the stage of 20 mm. but is atrophied in one of 30 mm. The bridge is generally absent in adult *Xenarthra*, but is present in *Dasypus gymnurus* (Albrecht). No case has been recorded in adult *Xenarthra* in which the interarytenoid bridge persists as a separate C. interarytenoidea s. intermedia. In this respect *Xenarthra* present a marked contrast to Marsupials and Monotremes. In *Manis* the primordium of the laryngeal muscles is formed as a postbranchial structure separated off from the primordium of the Constrictor oesophagi, migrates forward into the laryngeal region, and there develops into the Laryngeus dorsalis, Laryngeus ventralis, and Dilatator laryngis. In this *Manis* agrees with the pig. The corresponding stages of *Tatusia* were not available.

Knowledge of the laryngeal muscles in *Xenarthra* and *Manidac* is but slight. Incomplete accounts were given by Murie of *Tolypeutes*, and by Albrecht of *Dasypus septemcinctus*, *D. gymnurus*, *D. villosus*, *Bradypus didactylus*, *Myrmecophaga*, and *Manis gigantea*. The best description is that by Bender of *Tamandua*. The conditions found in *Tatusia* and *Manis javanica* may be compared with these. It would appear that (1) the Dilatator laryngis s. Crico-arytenoideus posticus always remains single. It does not separate into inner and outer portions as in Marsupials. (2) The Laryngeus dorsalis s. Inter-



arytenoideus passes from the C. arytenoidea to a dorsal median raphé. (3) The Laryngeus ventralis is very variable in subdivision.

(a) A Crico-arytenoideus lateralis is developed in *Tatusia novemcincta*, *Dasypus septemcinctus*, Tamandua, and also, judging from Albrecht's figures, in *Dasypus villosus* and Myrmecophaga, but not in *Manis javanica*. It is not known whether it is developed in *Manis gigantea*, *Bradypus didactylus*, and *Dasypus gymnurus*.

(b) The Thyro-arytenoideus remains single in *Manis gigantea*, *Dasypus septemcinctus*, and *Bradypus didactylus*. It becomes more or less separated into Thyro-arytenoideus superior and inferior in *Dasypus gymnurus*, *D. villosus*, Myrmecophaga, Tamandua, *Tatusia novemcincta*, and *Manis gigantea*.

The above recorded observation and discussion suggest that the following features characterise the cranial muscles of Xenarthra. (1) A Pterygo-tympanicus is generally present (it has not been recorded in Myrmecophaga and Chlamyphorus). (2) A homologue of the Detrahens mandibulae is perhaps present in Tamandua, Dasypus, and Tolypeutes. (3) A Mandibulo-auricularis is commonly present. (4) The Interhyoideus arises from the C. hyale in Tolypeutes and Chlamyphorus. Its origin extends up to the skull in other genera, and the muscle may undergo subdivision into upper and lower portions. (5) The Dilator laryngis s. Crico-arytenoideus posticus remains single. (6) A Sterno-mandibularis is present. It is formed by attachment of the Digastricus anterior to the transverse aponeurosis of the Interhyoidei and rotation of the muscle into a longitudinal position, the separation of a Sterno-hyoideus superficialis from the Sterno-hyoideus and attachment of its anterior end to the transverse aponeurosis. The resulting primary condition present in Bradypus, Choloepus, and Tolypeutes, is a Sterno-mandibularis with an intersection. The intersection is lost in other genera and the muscle becomes a continuous one.

The characteristics of the cranial muscles of Manidae are: (1) Fusion of the Sterno-hyoideus and Hyo-glossus, forming a Sterno-glossus. (2) Backward extension of the Sterno-glossus and Sterno-thyroideus in the thorax. (3) Backward extension of the Genio-hyoideus, and in less degree of the Transversus linguae, forming ventral and dorsal inner sheaths for the Sterno-glossi. (4) Backward extension of the Intermandibularis, with attachment of its posterior part to the base of the skull, forming an outer sheath for the fore part of the Sterno-glossi. (5) In *Manis javanica*, and possibly also in *Manis tricuspidis* and *macrura*, backward extension of the Interhyoideus, forming an outer sheath for the hinder part of the Sterno-glossi. (6) Transformation of the Tensor tympani and Digastricus anterior into protractors of the hyoid bar and salivary gland. (7) Formation of both Pterygo-tympanicus and Tensor veli palatini. (8) Atrophy of the Pterygoideus internus. (9) Formation of a Zygomatico-mandibularis. (10) Formation of an Occipito-humeralis. (11) Non-formation of a Cleido-mastoideus. (12) Formation of a Mandibulo-auricularis. (13) The Stylo-pharyngeus forms a Dilator pharyngis. (14) Non-formation of a



Branchio-hyoideus. (15) Non-formation of a Transversus hyoideus and Hyo-epiglotticus.

Manidae thus possess the characteristic Xenarthric feature of a Pterygo-tympanicus, but not that of a Sterno-mandibularis, and there are many secondary features correlated with the great development of the tongue and the absence of a clavicle.

I have the pleasure of thanking Prof. Fawcett for the loan of the sections of Tatusia, and Prof. de Lange for the loan of the sections of Manis and of Erinaceus.

The expenses of the illustrations have been defrayed by the Colston Research Society.

#### SYNONYMS

*Interhyoideus*. Stylo-hyoideus, Stylo-hyoid, Stylo-hyoïdien. Hyrtl, Macalister, Chaine, Burne (Chlamydophorus). Toldt (Manis).

Digastricus, hintere Bauch. Toldt (*Dasypus villosus*, Tatusia, *Bradypus tridactylus*, *Tolypeutes*).

Ventre postérieure du digastrique. Chaine (*Dasypus villosus*, Tatusia, *Bradypus tridactylus*).

Venter posterior M. digastrici. Bijvoet (*Bradypus tridactylus*).

Portion of Glossovaginalis superficialis arising from bulla tympanica s. Stylo-hyoideus. Ehlers (Manis).

*Interhyoideus dorsalis*. Mastoideo-hyoideus. Schulman (Choloepus, Tamandua). Stylo-hyoideus. Owen (Myrmecophaga). Toldt (Tamandua). Stylo-mastoideus. van Kampen (Tatusia). Stylo-mastoidien. Pouchet (Myrmecophaga).

*Interhyoideus ventralis*. Styloideus. Schulman (Choloepus Tamandua). Cerato-hyoideus. Owen (Myrmecophaga). Stylo-hyoïdien. Duvernoy and Pouchet (Myrmecophaga). Mylo-hyoideus, superficial layer. Toldt (Tamandua).

#### LIST OF FIGURES

The figures are taken from sections cut in a frontal plane except in the case of Nos. 29-31, which are from transverse sections. In any series from an embryo the one with the lowest number denotes the uppermost, or the most anterior, section drawn.

##### *Tatusia novemcincta*. Figs. 1-31

- Figs. 1-5. Embryo 10 mm. vertex-breech length.
- Figs. 6-16. Embryo 12 mm. vertex-breech length.
- Figs. 17-19. Embryo 17 mm. vertex-breech length.
- Figs. 20-28. Embryo 20 mm. vertex-breech length.
- Figs. 29-31. Embryo 30 mm. vertex-breech length.

##### *Manis javanica*. Figs. 32-63.

- Figs. 32-36. Embryo 8.5 mm. (A) vertex-breech length.
- Figs. 37-39. Embryo 8.5 mm. (B) vertex-breech length. (This embryo, though of the same size as (A), is slightly more advanced in development.)
- Figs. 40-44. Embryo 10 mm. vertex-breech length.
- Fig. 45. Embryo 13 mm. vertex-breech length.
- Figs. 46-53. Embryo 14 mm. vertex-breech length.
- Figs. 54-58. Embryo 18.5 mm. vertex-breech length.
- Figs. 59-63. Embryo 21 mm. vertex-breech length.

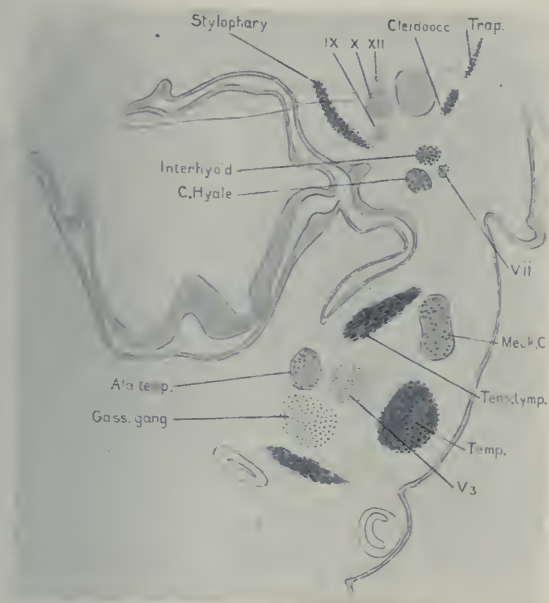


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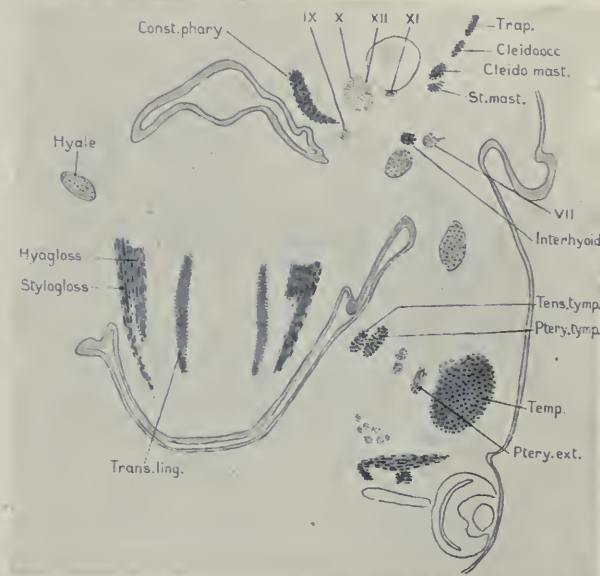


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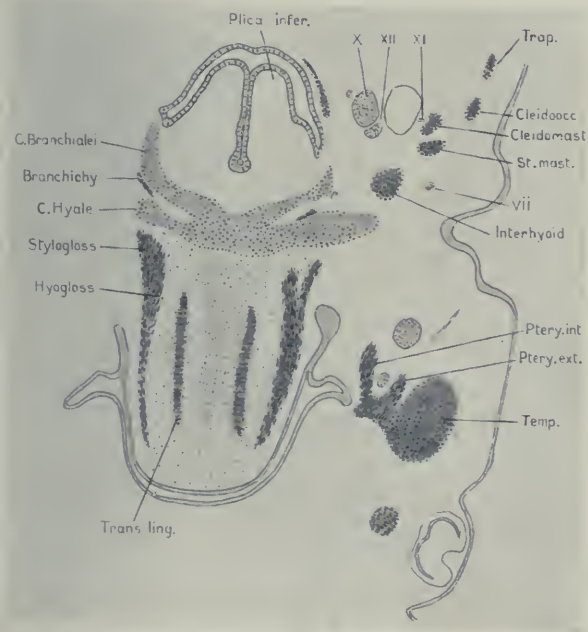


Fig. 3

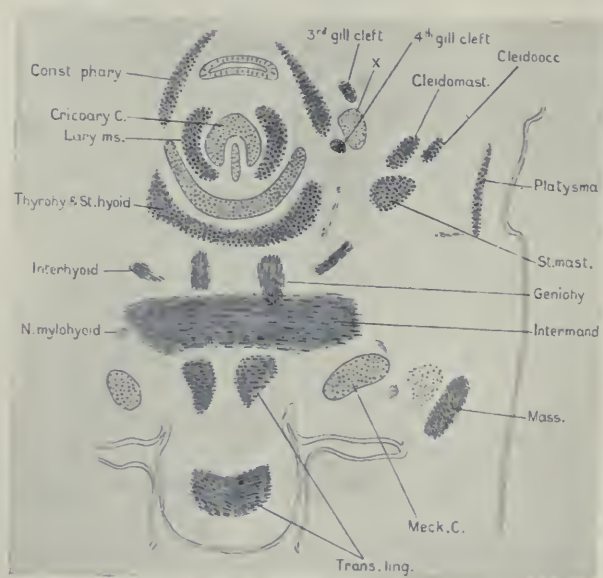


Fig. 4

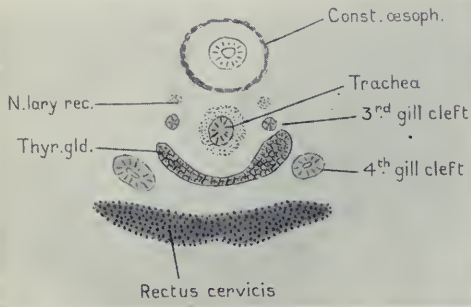


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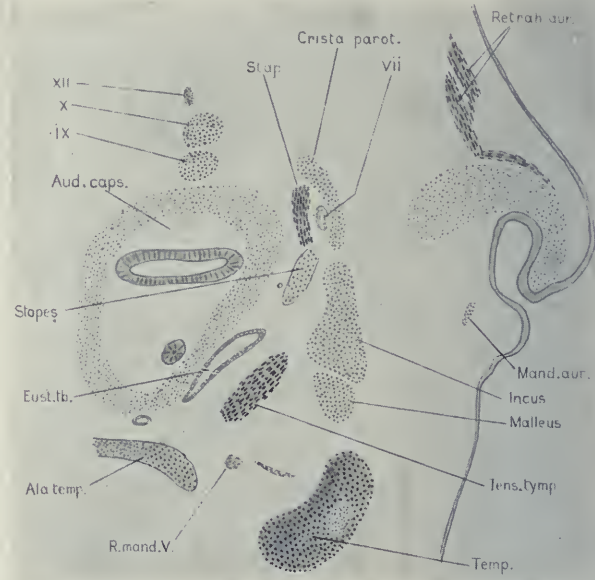


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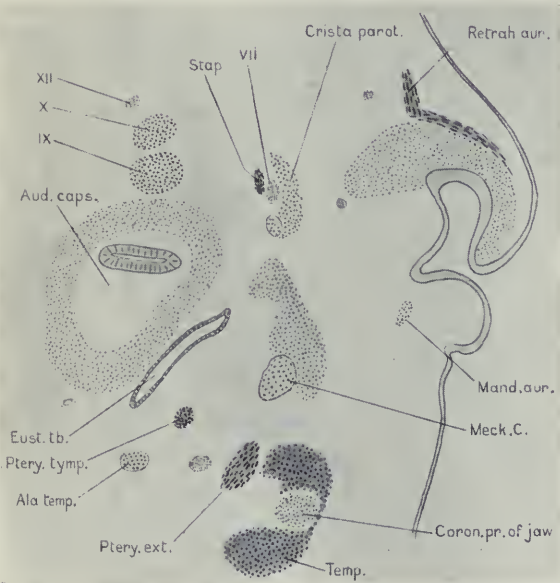


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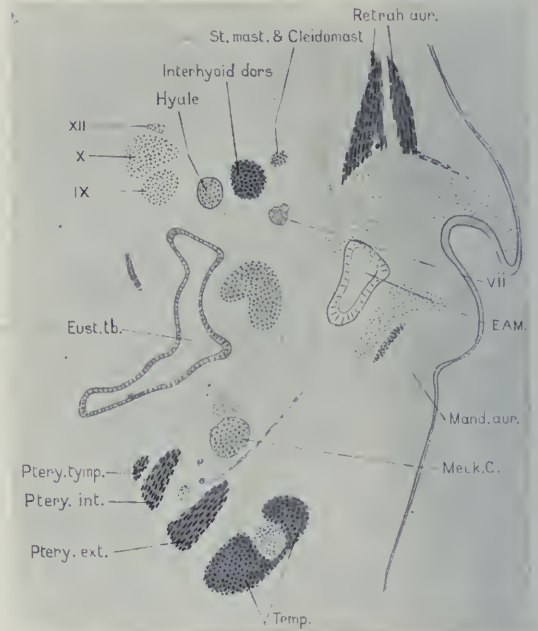


Fig. 8



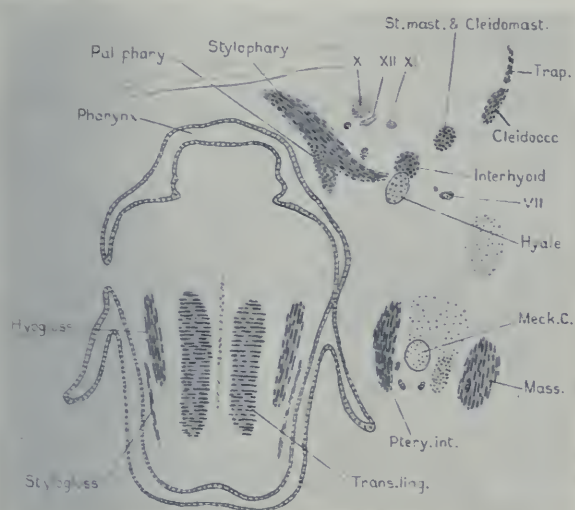


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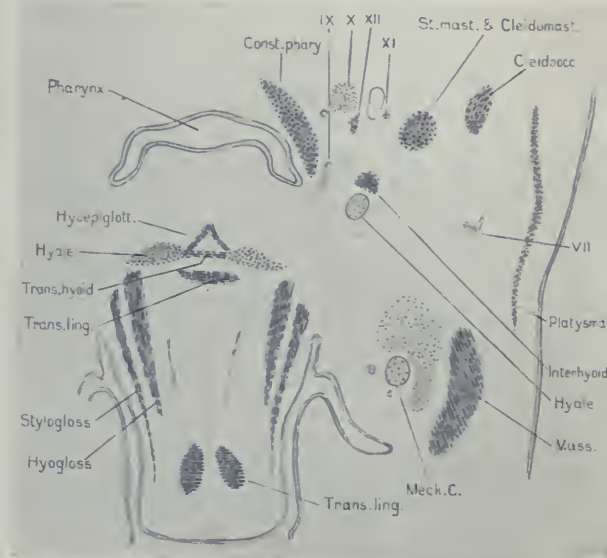


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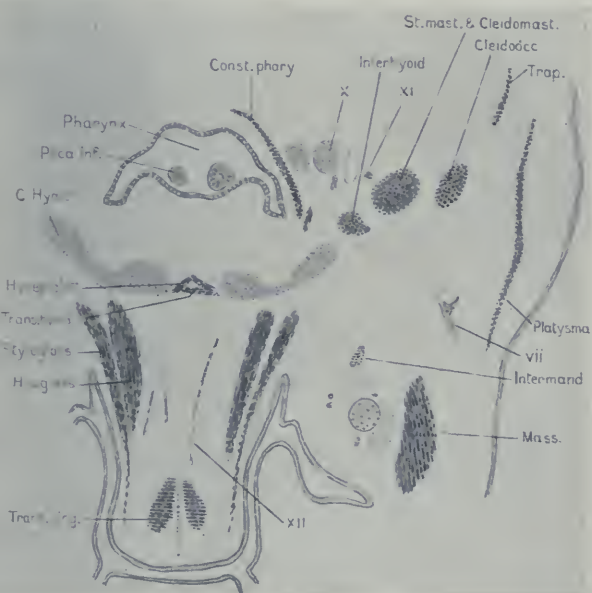


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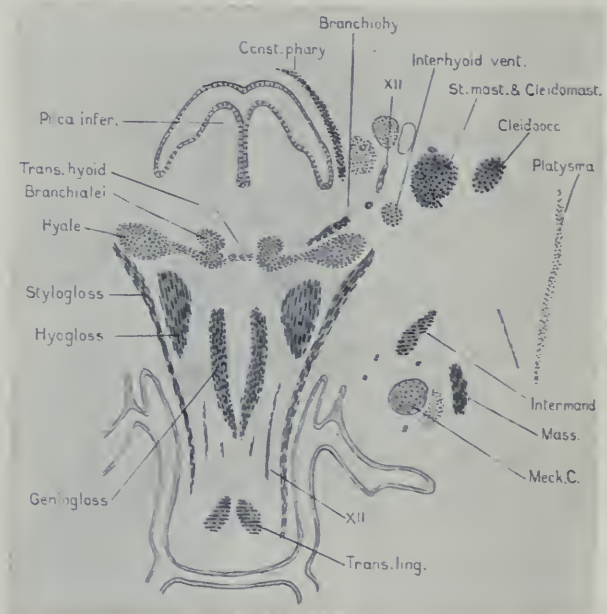


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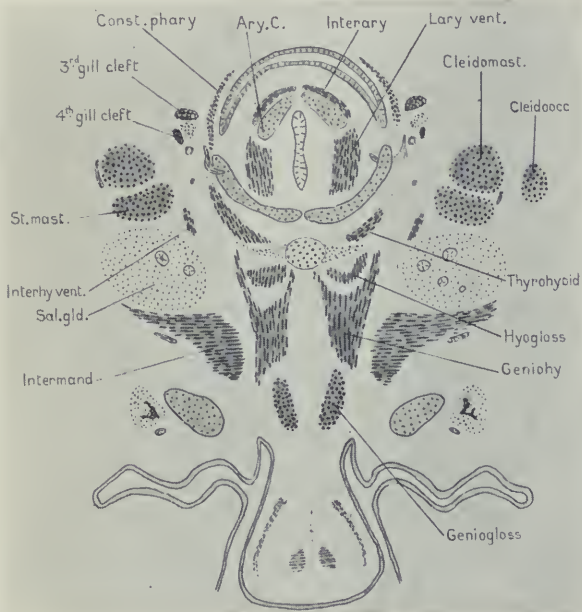


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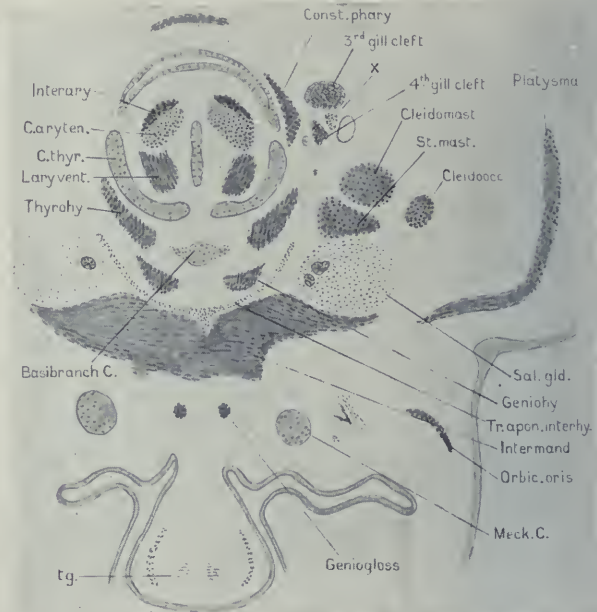


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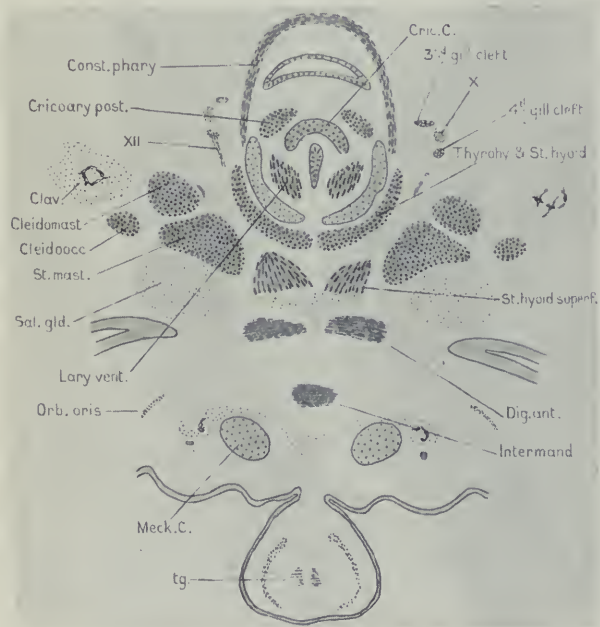


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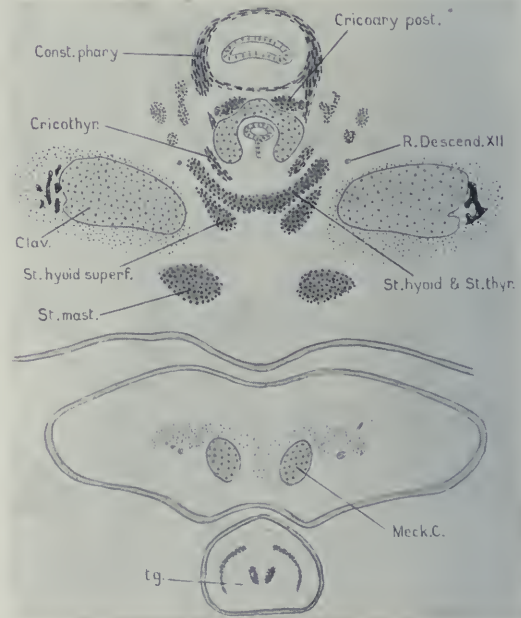


Fig. 16

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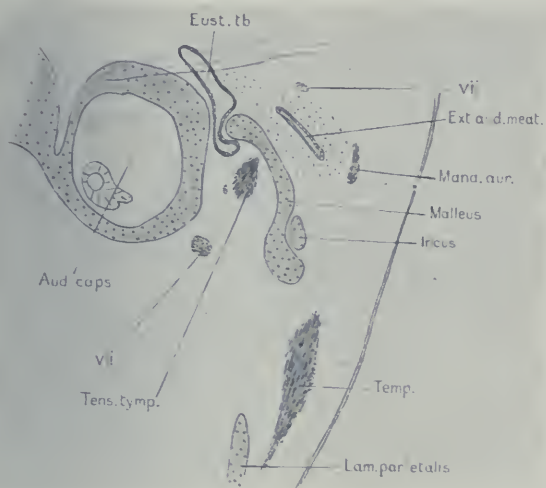


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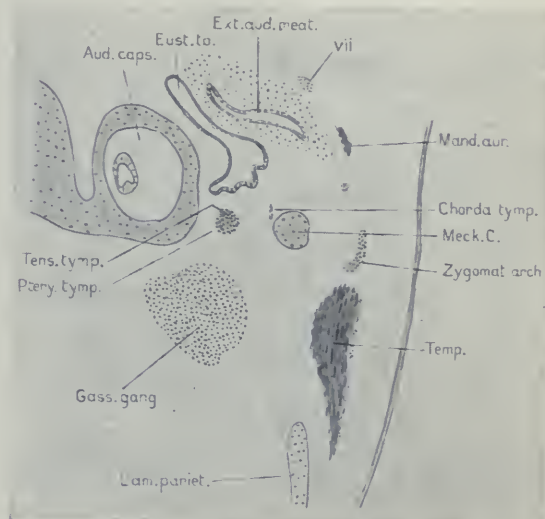


Fig. 18



Fig. 19

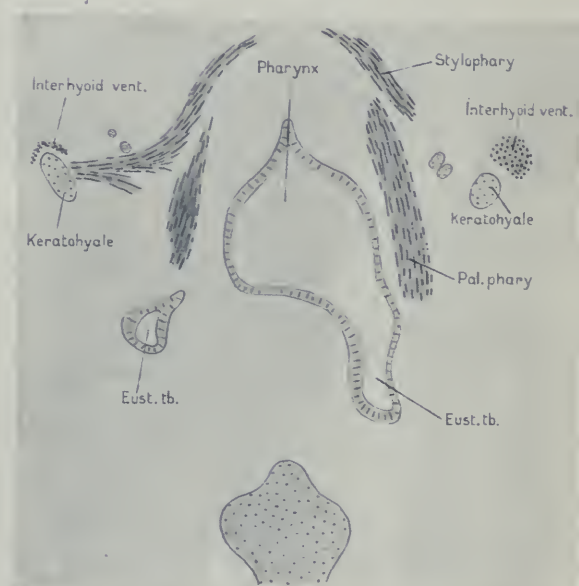


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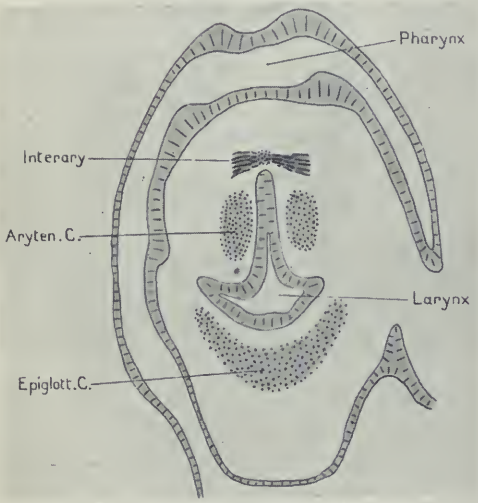


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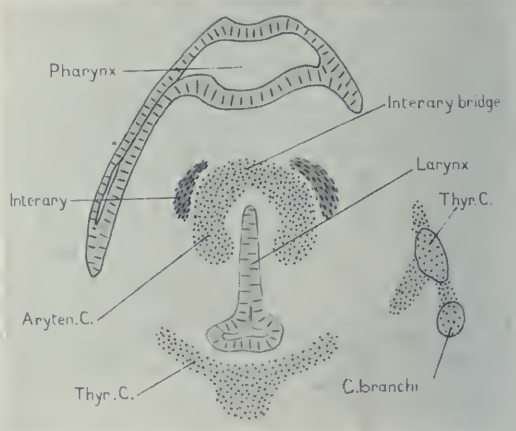


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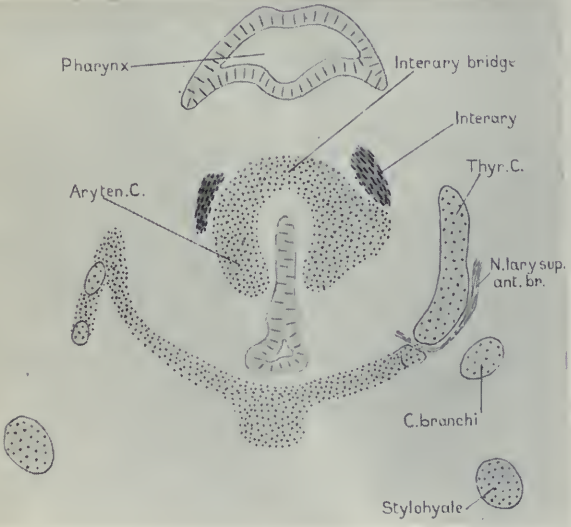


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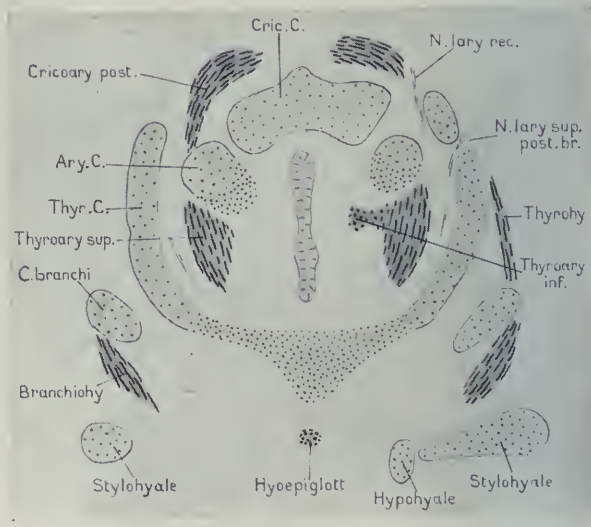


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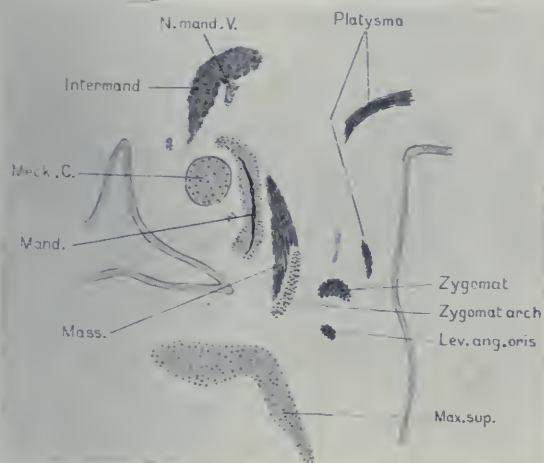


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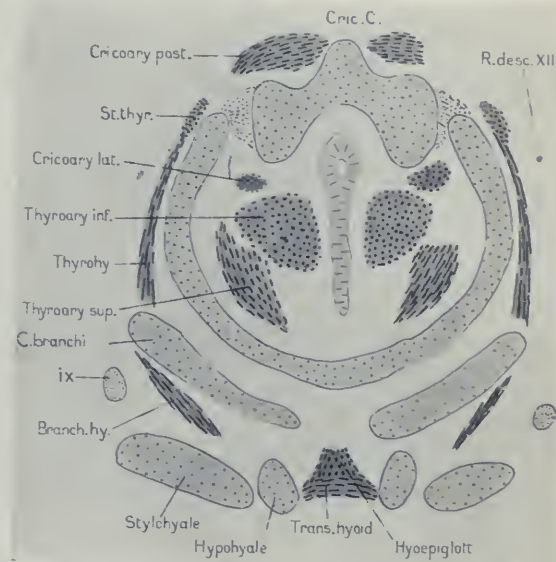


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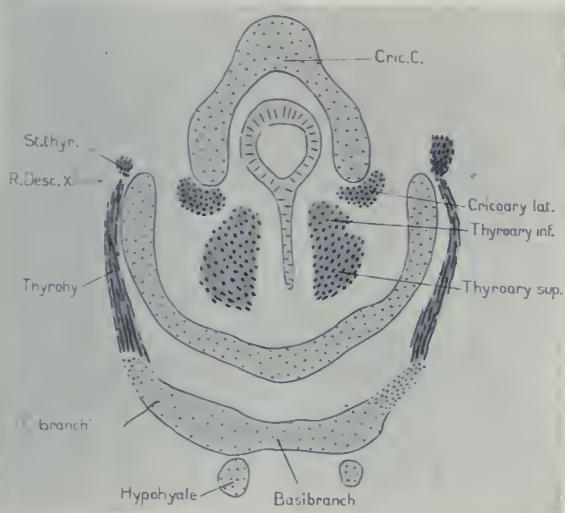


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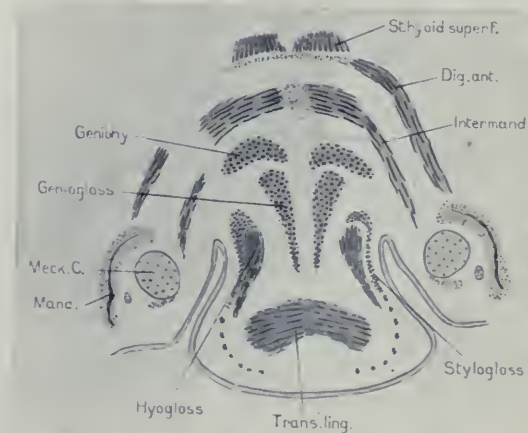


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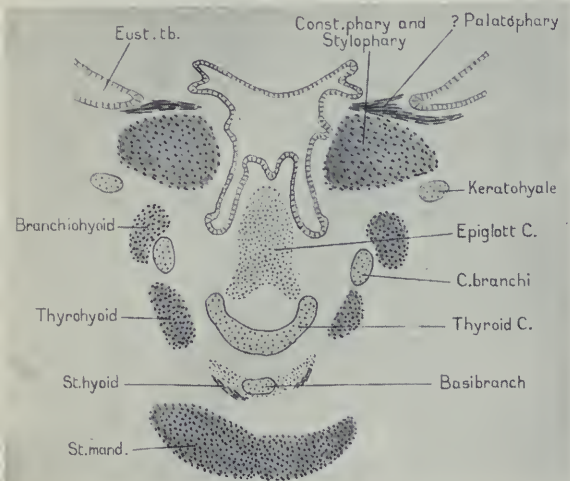


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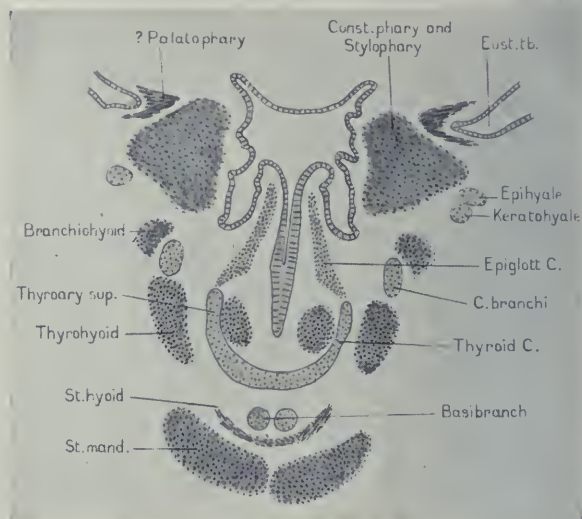


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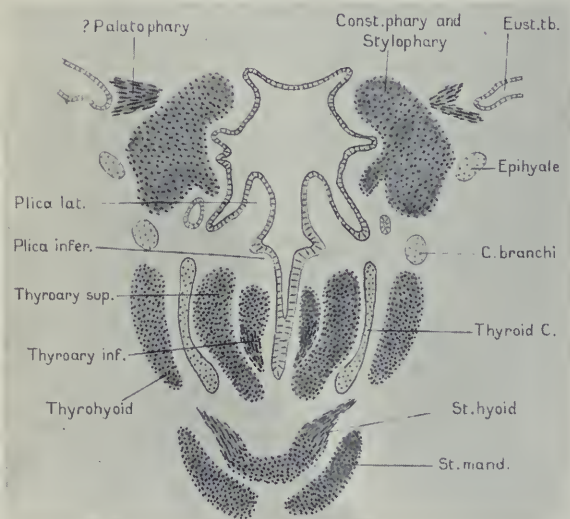


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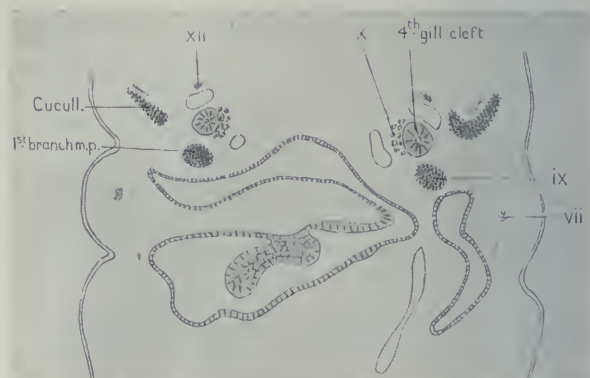


Fig. 32



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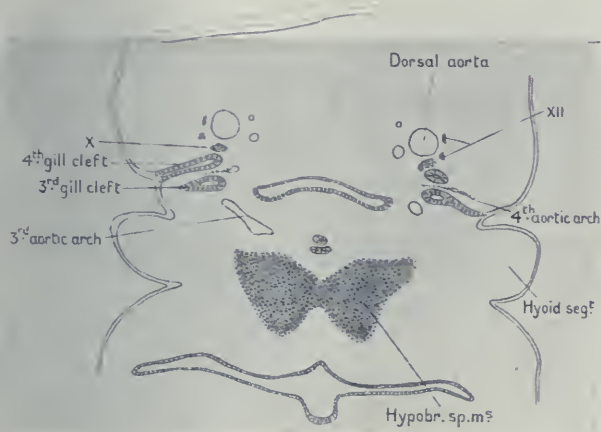


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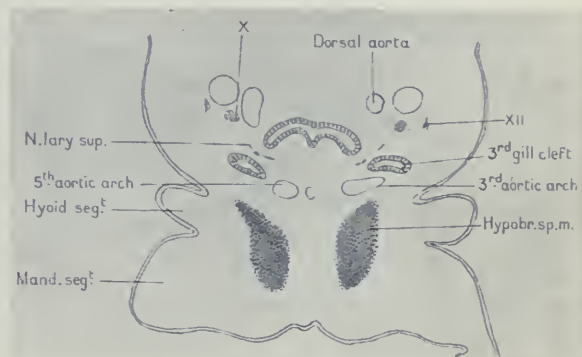


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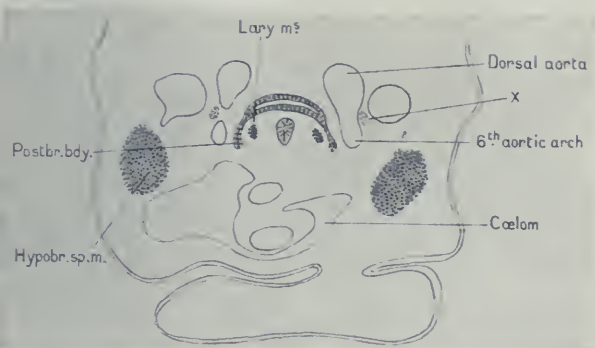


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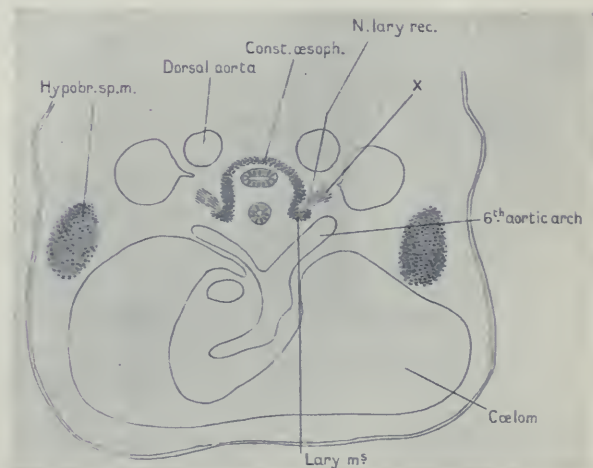


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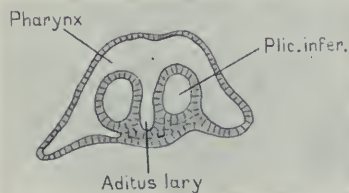


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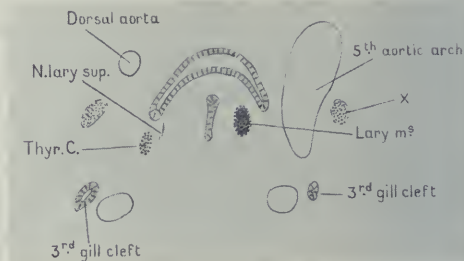


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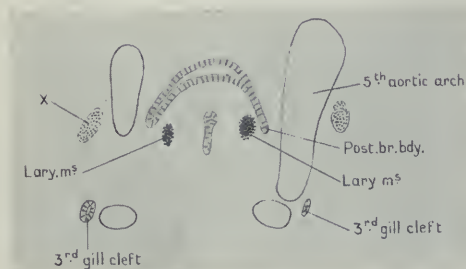


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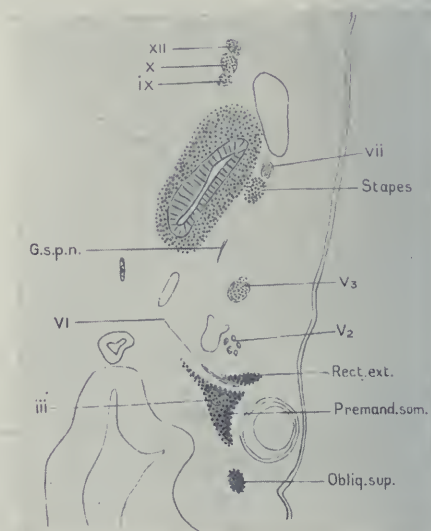


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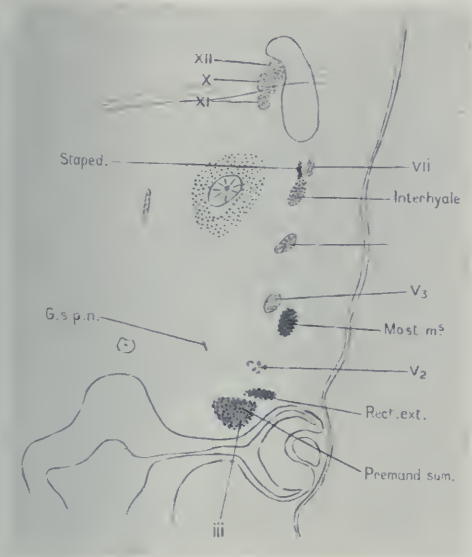


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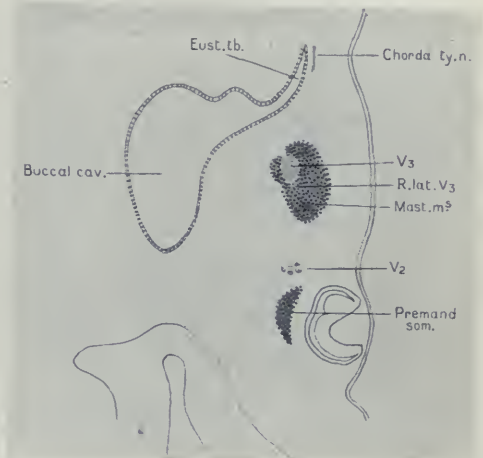


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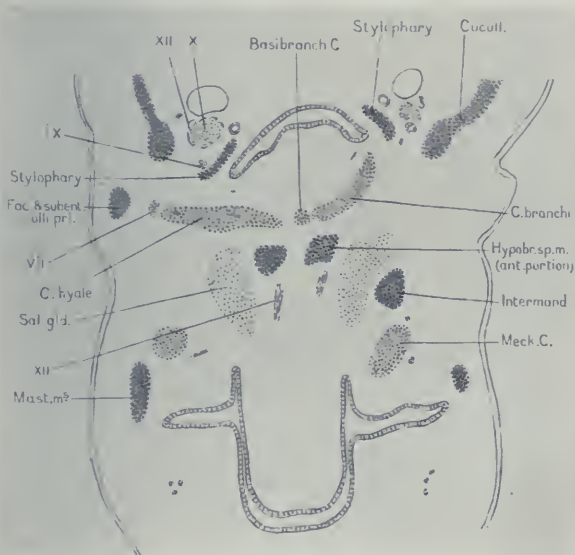


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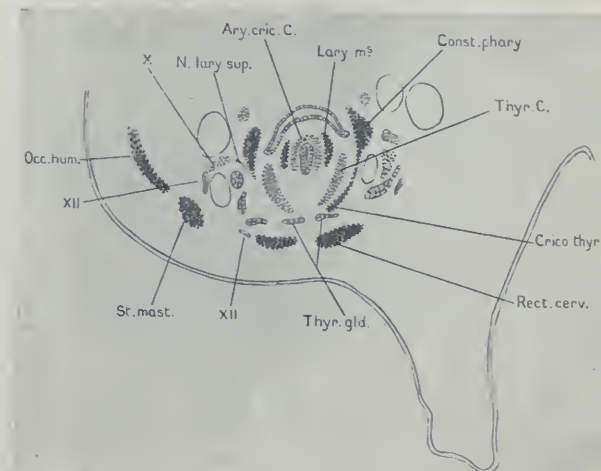


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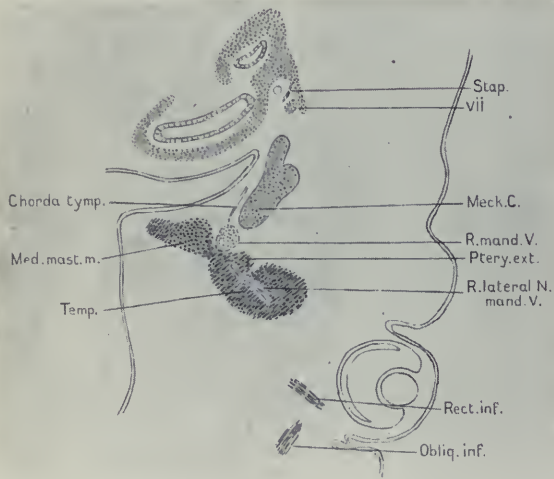


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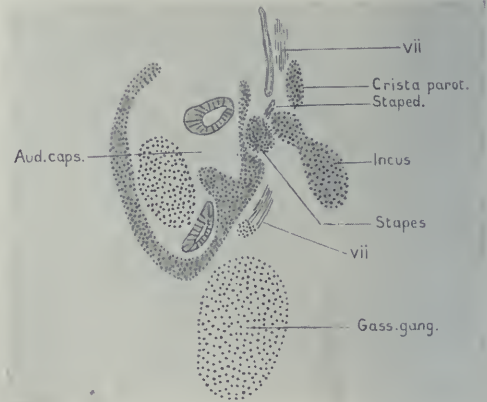


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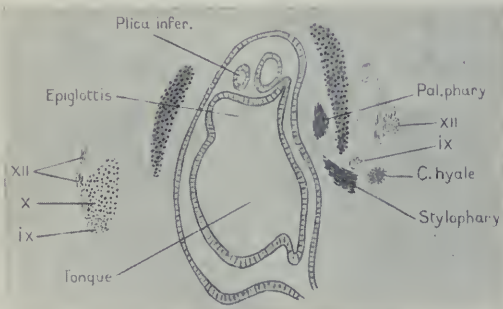


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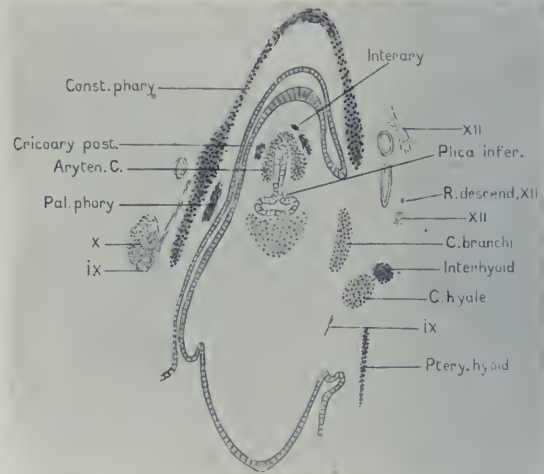


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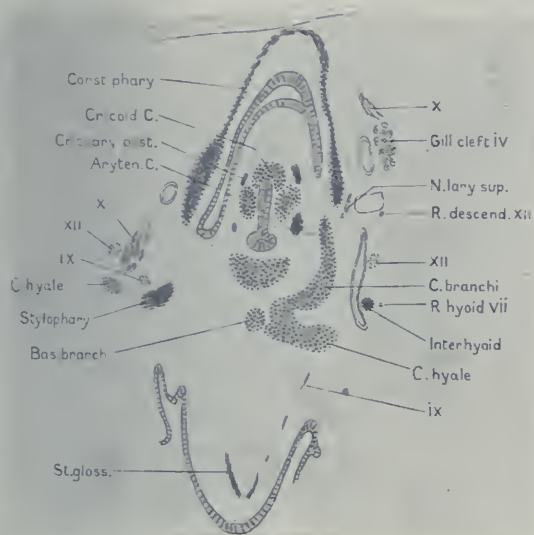


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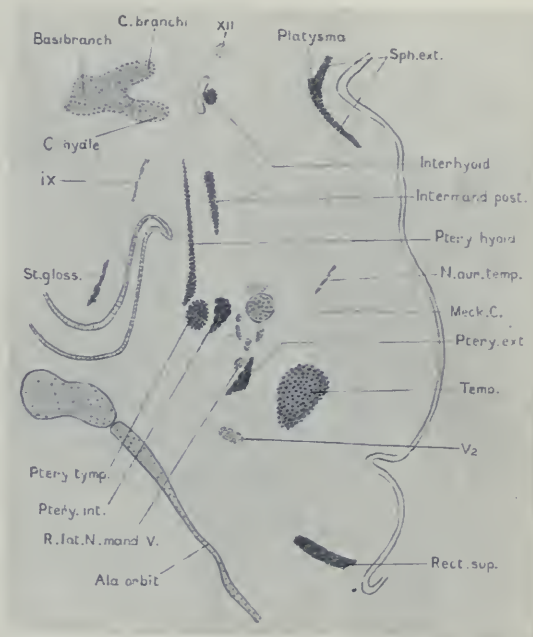


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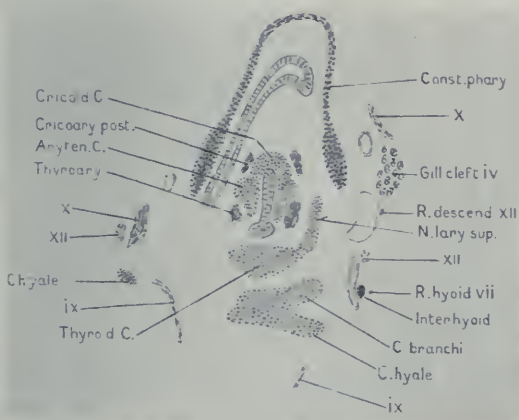


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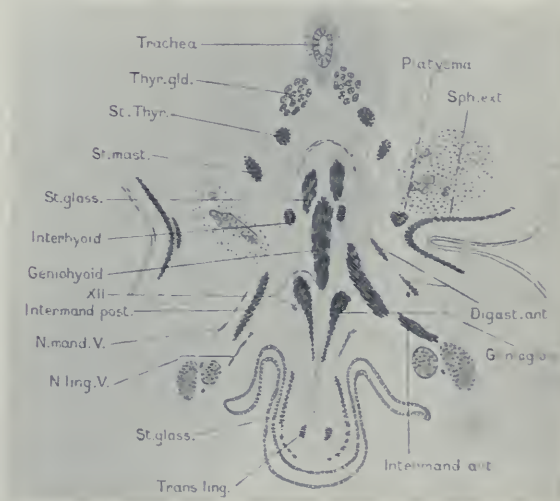


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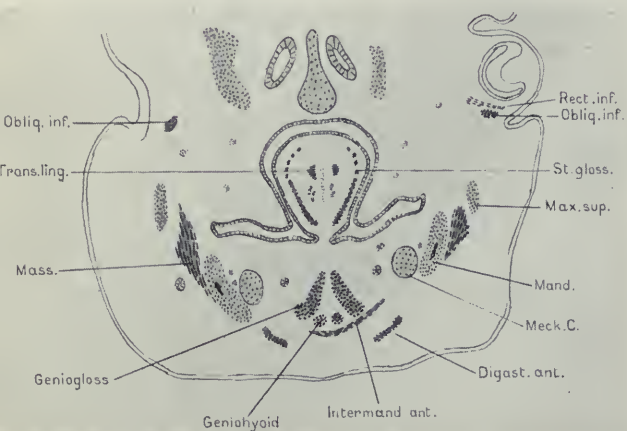


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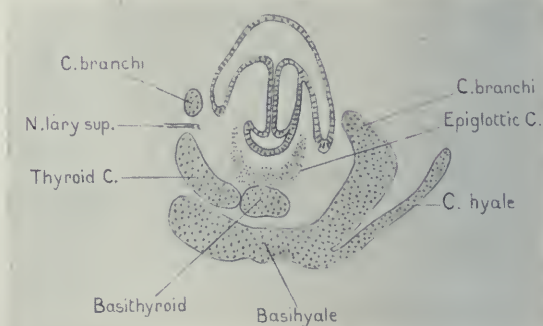


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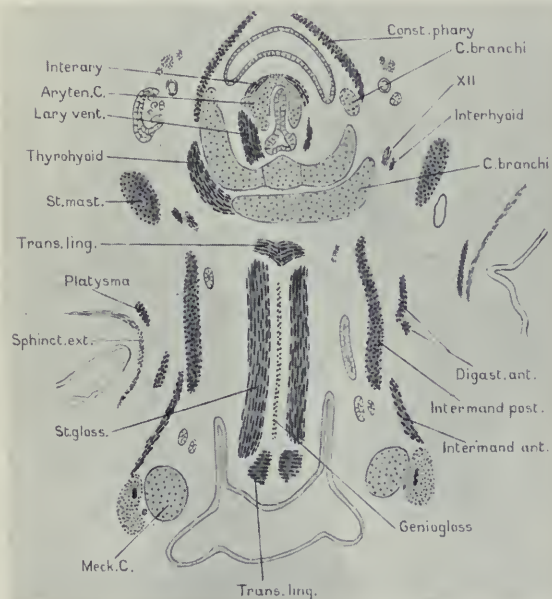


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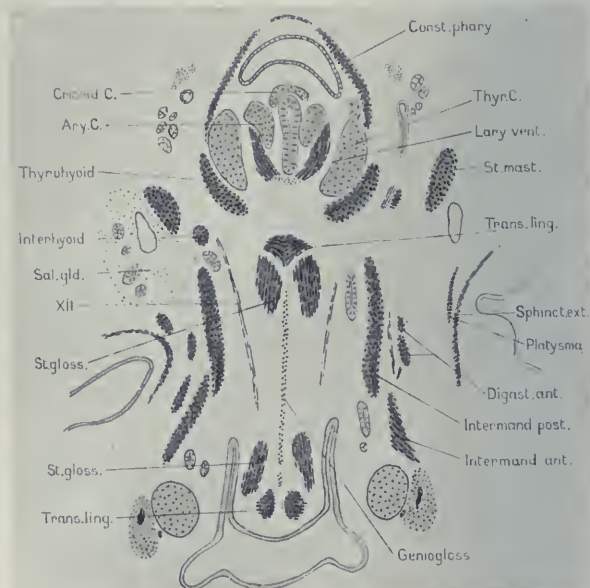


Fig. 56



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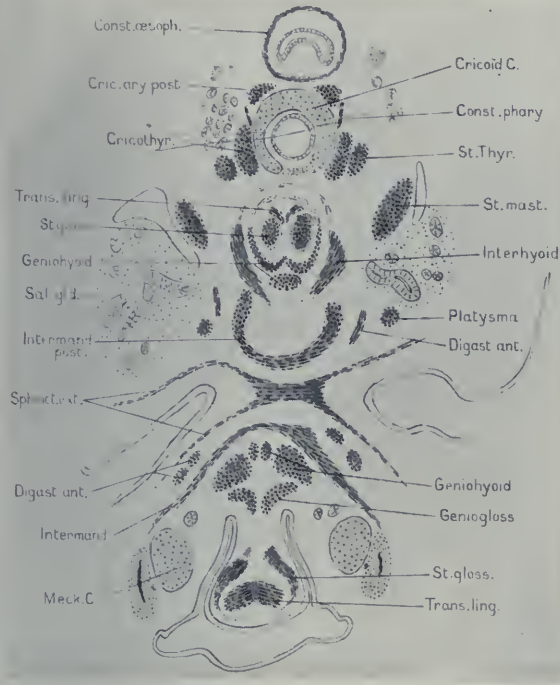


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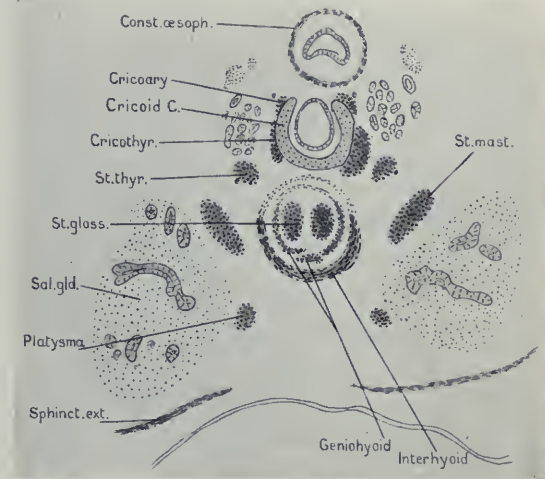


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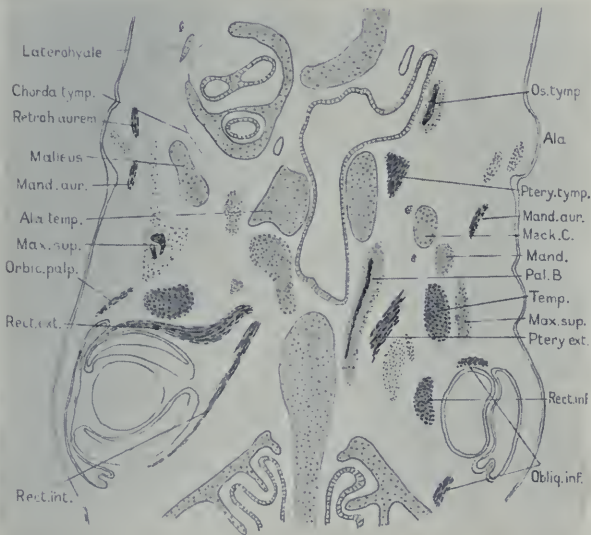


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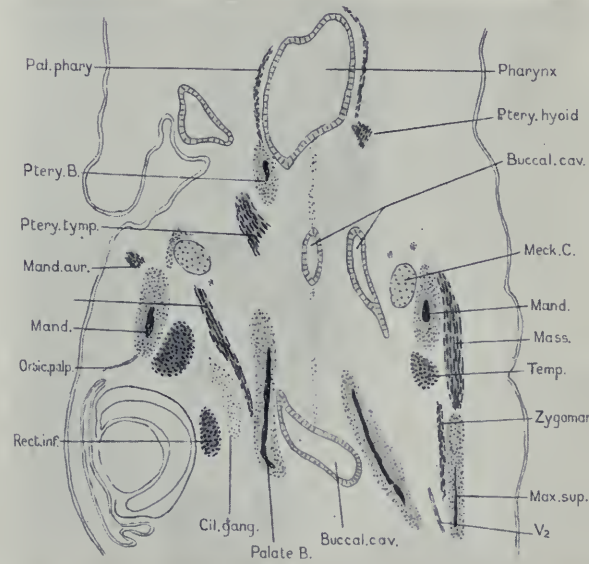


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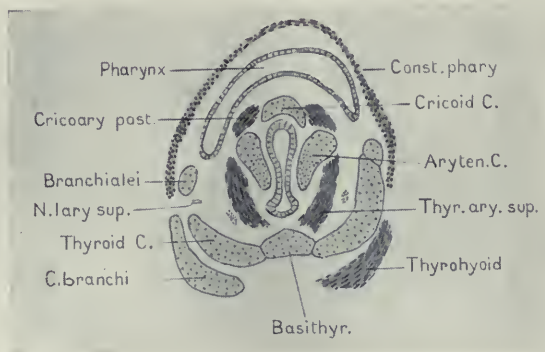


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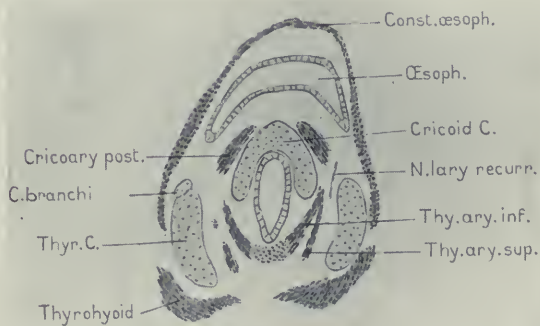


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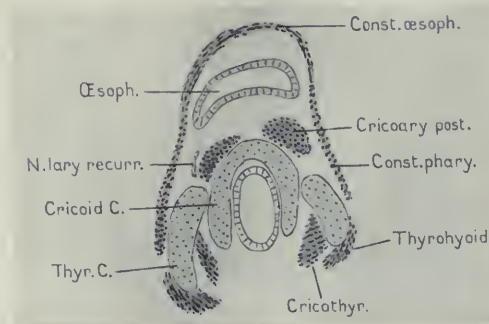


Fig. 63

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# THE EFFECT OF MACERATION AND DRYING UPON THE LINEAR DIMENSIONS OF THE GREEN SKULL

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## INTRODUCTION

IN a former and larger work<sup>(8)</sup> I have discussed in a preliminary manner the influence of drying upon the linear dimensions of the cranium. When one attempts to obtain an approximation of true cranial capacity from dimensions of the living skull one must make corrections for certain errors. Of these the error resulting from estimation of the thickness of the soft tissues will not concern us at the moment. Since all really serviceable computations of cranial capacity made strictly in accordance with statistical theory have been based upon dimensions obtained from dried specimens it is plainly necessary to form some idea of the shrinkage taking place in all the basic dimensions as a result of drying. It may be objected that estimation from living values does not permit an approximation close enough to allow one to hope for a greatly increased accuracy even if this small correction is obtained because there are many factors still at work limiting the probable accuracy in individual cases. We have already mentioned the superficial soft parts. In addition there are the volume of the dura and the thickness of the skull bones as well as peculiarities in conformation of the head itself. It is not beyond hope that in time all these sources of error may be minimised. Some work has already been done upon the thickness of the soft parts; I have taken up in considerable detail the problem of the dura volume<sup>(8)</sup>: it is possible that eventually we may have some fair guide to the probable average thickness of the skull bones; variations in the conformation of the head do not inject a very considerable error even for

the individual except in rare instances which are usually obvious. As far as racial values of the dried skull are concerned it has been shown beyond a doubt that even with present limitations an accuracy of computation of capacity can be obtained as great as or greater than that resulting from direct capacity determination by an experienced observer. This in itself encourages the expectation that with proper corrections it may soon be possible to obtain a result of at least comparable accuracy from living measurements. After all it is the anatomy of the race and particularly of the living race that will mostly concern us in the future. No further justification is needed for the investigation of problems in living anatomy.

If there is to be any success in this newer field of living anatomy now rendered possible by clinical methods devised in recent years the work must be done in the Hospital and Medical School where the same individual is under observation both before and after death, rather than in the Museum or the Institute remote from the Clinic. In very many problems such as that under consideration, namely cranial capacity, the Anatomical Department is, up to the present, directly responsible for the paucity of organised data, for surely there, if anywhere, a wealth of material has passed to final extinction, serving merely to equip students in traditional manner with the rudiments of the subject. The increasing difficulty in obtaining anatomical material makes it increasingly evident that material must be utilised to greater advantage and the claim really made good that it is the introduction to a broader, essential and vital anatomy of the quick rather than merely of the dead.

#### HISTORICAL SURVEY

So far as I am able to discover there has been no work done upon the initial shrinkage of bones in drying. It is true that Welcker, Broca and Pearson have made observations upon the effect of moisture and of subsequent drying upon the dimensions of the previously dry skull and of the femur. This is not exactly the same problem and although it is a valuable addition to our knowledge it does not give us the confidence of first hand information upon the change consequent upon transformation of green bones into dry bones.

Pearson's work<sup>(7)</sup> refers to the femur and as such does not come directly within our purview. Welcker published his investigation upon the skull in a volume which unfortunately is inaccessible to me<sup>(9)</sup> but I have beside me the study of Welcker's observations and deductions made by Broca<sup>(1)</sup>, a study which bears the ear-marks of all Broca's faithfulness to detail and fairness in statement when in the position of an opponent. Broca used solely dried skulls which he subjected to varying degrees of humidity and to total immersion in water. Welcker had certainly observed green skulls for he made the statement that if a green skull be bisected and then macerated the two halves no longer correspond. With this observation I do not find myself in agreement. All our skulls are bisected green and then macerated by Leonhart's live steam method. There have now passed through our hands some nine hundred skulls

and not once have we found a specimen in which the two halves do not exactly correspond at all stages of drying. I can only conclude that the skulls referred to by Welker were macerated by a very imperfect method, a view which appears to have been shared by Broca (1, p. 68).

According to Broca, Welker found that after three successive days' soaking in water an adult human skull undergoes the following average increases in cranial dimensions: length 0.4 mm.; breadth 0.7 mm.; basio-bregmatic height 0.7 mm. This, of course, is practically negligible as most series of measurements are by the nature of the instruments used, not correct to less than 0.5 mm., and ill accords with Welker's own statement regarding the non-correspondence of two halves of a skull macerated after bisection, unless indeed my contention be allowed that a crude method of maceration was employed.

Broca himself found an increase of some 30, 40 or even 50 c.c. in capacity as the result of soaking the skull whereas the linear extensions given by Welker increase the capacity by only 18.98 c.c. on Broca's method of computation. Considering the delicacy of measurement of so relatively slight a change in dimension Broca suggests that perhaps an error of 0.3 or 0.4 mm. may have crept into Welker's estimates and that this correction would bring the results of the two investigations into harmony.

In my previous work<sup>(8)</sup> I have endeavoured to ascertain the shrinkage of ten male White skulls as the result of drying for a period of more than a month in the dry atmosphere of our steam-heated Museum. Having allowed for the instrumental error my results are the following: length 2.3 mm.; breadth 2.25 mm.; auricular height 1.8 mm. This is a very great increase upon the changes determined by Welker. The question which therefore presented itself to me was whether the initial shrinkage is so much greater than the extension obtained by soaking the dry skull or whether more delicate instruments would show that I had exaggerated the amounts. I have already shown that this shrinkage in a skull of about 1500 c.c. capacity amounts to a difference of 47 c.c. which is within the range anticipated by Broca and accords very well with my own direct determinations. Nevertheless the problem seemed worthy of a more intensive study and it is the result of this study which I now present.

#### TECHNICAL METHODS AND THEIR CONTROL

In a piece of work requiring such accurate measurement the instruments used must be very carefully tested. The preliminary investigation which I have already published showed me the vital necessity of instruments with a smaller error than I was then using<sup>(8)</sup>. For holding the skull and measuring the auricular height I have employed a modification of Ranke's Craniophor (Pl. I) and for measuring greatest length, Pearson's Blocks (Pl. II), both instruments being made in the laboratory by our Mr Cherney. The instruments are mounted upon millimetre paper fixed to a drawing-board by Martin's



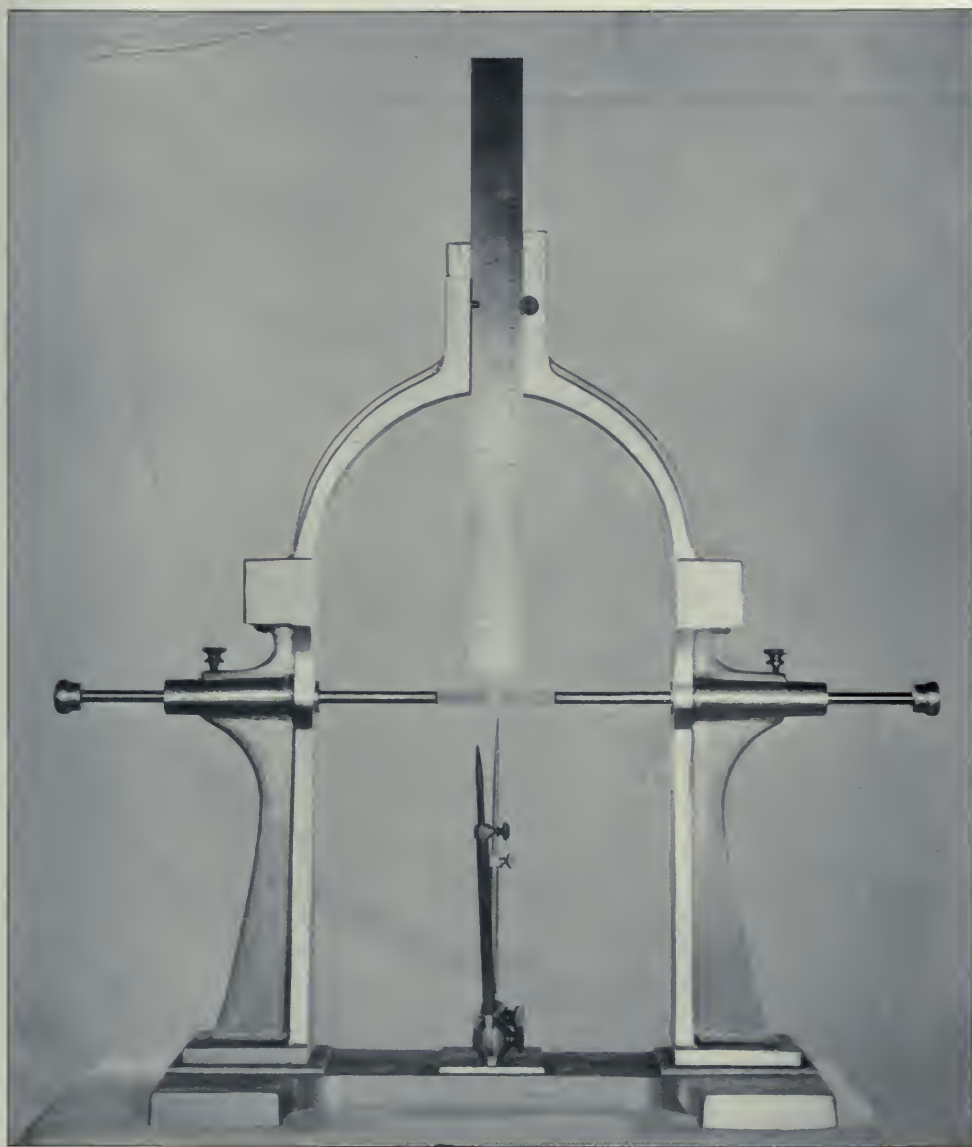


Fig. 1. The Reserve Craniostat as seen from the front.

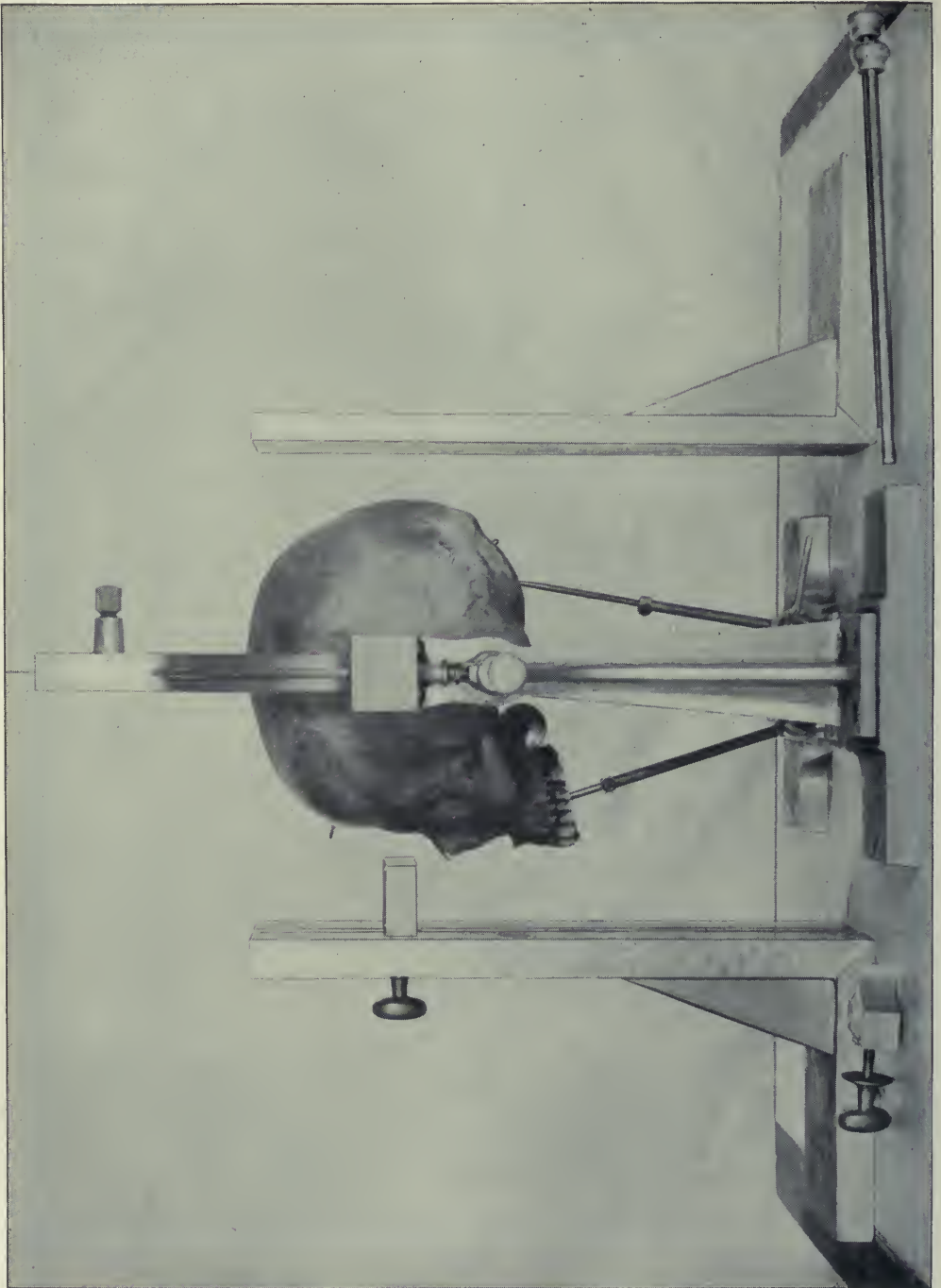


Fig. 2. Reserve Craniostat and Cambridge (Pearson's) Blocks mounted upon millimetre paper. By the former the auricular height is determined. The Blocks give greatest length. In this illustration the front block has mounted upon it the flat aluminium projection for determining greatest length including supereiliary ridges (see Fawcett (2)).

celluloid cement (6, p. 32) and varnished with the same material. This millimetre paper has been carefully checked up with a Flower's craniometer manufactured by Aston and Mander, and with Martin's Gleitzirkel made by Hermann. The skull is oriented in the Frankfort plane by the aid of a Spengler's pointer (*Horizontiernadel*) and both glabellar length and greatest length including superciliary ridges read off with the assistance of the blocks. The auricular height is taken twice, first with the skull mounted on the knife edge supports (see fig. 1) and next mounted on the rounded rods. (These rods may be seen lying on the base in fig. 2.) By this double measurement of each dimension I have sought to eliminate gross errors of reading and to minimise fine ones of technique. The breadth is taken as usual with Flower's craniometer and the site of greatest breadth recorded. After very careful checking, the demonstration of which need not be entered into here, I am disposed to accept the recorded measurements without further correction such as I felt compelled to adopt in my earlier work (8). The saw-cut needed for the bisection of the skull when green does not concern us since the initial measurement of breadth in this investigation is obtained subsequent to that operation.

The last series of skulls to pass through the macerator for the year 1922, twenty-four in all, I have measured within twelve hours after emergence from the macerating tank (some delay being advisable to permit of draining), and at intervals of a week thereafter. The work started on May 12 and continued until July 14. On August 18 and 19 I repeated all measurements and am therefore able to state the shrinkage occurring during this period. None of the skulls has been subjected to the dry steam heat of the building during the Spring months so that one is able to compare results with those of the former research carried out during the Winter. The drying influence has been the ordinary Summer heat with the normal fluctuation in humidity. The skulls fall into two series, a larger one of twenty specimens emerging from the macerator on Tuesdays and a smaller one of four skulls taken from the macerator on Fridays. It is therefore in the larger series that we are enabled to study the effect of the weekly changes in heat and humidity.

In order to abbreviate this report I do not propose to set out in full the measurements and detailed observations which this work has demanded but rather to prepare summaries of the results attained.

#### GENERAL FEATURES OF SHRINKAGE OF THE SKULL IN DRYING

In his consideration of the figures presented in this section the reader must recognise that the shrinkage being investigated is that of the macerated skull in drying. It is not the alteration in dimensions consequent upon the change from the green to the dried macerated skull.

Of the twenty-four skulls employed, there are eleven male Whites, four female Whites, six male Negroes and three female Negroes, this being the random sample of the last maceration for 1922. Table I gives the average



Table I. *Average final dimension and average shrinkage in mm. with percentage of latter on former.*

Row	No. of skulls	Sex and Stock	Length	Shrinkage	%	Breadth	Shrinkage	%	Auric. height	Shrinkage	%
1	11	M. W.	186.3	1.27	0.68	145.3	1.45	1.01	116.6	1.41	1.21
2	4	F. W.	174.1	1.25	0.72	132.6	1.87	1.41	111.6	1.50	1.34
3	6	M. N.	187.1	2.17	1.16	139.3	2.08	1.49	111.1	1.54	1.39
4	3	F. N.	178.2	1.50	0.84	133.5	1.83	1.37	110.4	1.75	1.58
5	24	Total	183.2	1.52	0.83	140.2	1.73	1.23	113.6	1.50	1.32
Measurements with "old apparatus" (see (8)) corrected.											
6	10	* M. W.	181.7	2.3	1.2	144.4	2.25	1.8	112.7	1.8	1.6
7		†	182.3	1.85	1.01	144.4	2.25	1.76	112.5	2.15	1.92
8		M. W.	182.1	1.2	0.66	145.5	1.55	1.06	115.25	1.95	1.70

The percentages are calculated on the complete figures, not on the above approximations to two decimals.

\* Figures obtained from previous investigation (see (8)).

† Figures obtained from new measurements (see text).

fully dried length, breadth and auricular height of each of the four series, together with the average shrinkage in millimetres of each dimension and the percentage of this shrinkage to the final dried dimension. Rows 6, 7, 8 of Table I refer to the shrinkage of green skulls. They will be interpreted later but are inserted here for convenience of comparison with the present results.

The length is the greatest length, the skull being measured with Pearson's blocks in the Frankfort plane and includes the superciliary ridges (see Fawcett's description(2)). Breadth is measured with Flower's craniometer. Auricular height is taken on the Reserve Craniophor (fig. 1), the skull being mounted on the rounded rods in the Frankfort plane. No instrumental corrections are made, repeated check observations having shown that none are called for with the instruments used upon the present series of skulls.

Row 5 gives the result of the entire group of twenty-four skulls. There is obviously no absolutely constant relation between shrinkage and the dimension in which that shrinkage takes place. It is worth noting that the percentage of shrinkage in length is less than the percentage of shrinkage in either of the two other dimensions. This immediately suggests a possibility of some relationship of shrinkage to patent sutures like the squamous. We shall consider this possibility later. At the moment we observe that this unexpected result confirms in principle that obtained by Welcker and indicated by my earlier investigations, a result which I formerly considered to be probably invalid.

Rows 1 to 4 confirm the apparently erratic nature of the shrinkage, but also give conclusive evidence of a shrinkage in breadth and height relatively greater than in length. The average reduction taken over the three dimensions is 1.1 per cent. This is distinctly more than was obtained by Welcker but less than the amount I previously obtained when working with green skulls. Hence to this and to the other puzzling problem of differential shrinkage we must return after more of the results are set forth.

## DURATION OF SHRINKAGE PERIOD

Table II presents the evidence obtained for the actual amount of shrinkage per week. Since all the skulls were not macerated at one time the total number diminishes as the number of weeks increases. There are, however, sufficient

Table II. *Average shrinkage by weeks in millimetres. Average length 183.5 mm.; average breadth 140.2 mm.; average auricular height 113.6 mm.*

Week (end of)	No. of skulls	Length	Breadth	Auricular height
1st	24	1.21	.65	.91
2nd	24	.15	.29	.32
3rd	24	.17	.31	.09
4th	24	.12	.12	.09
5th	22	+ .07	.27	.04
6th	14	.14	.04	.12
7th	11	+ .14	.04	0.0
8th	5	.10	0.0	+ .10

The plus sign ( + ) indicates an actual average increase in the dimension instead of the customary reduction. This is probably due to changes in atmospheric humidity (see text).

data to indicate the duration of the shrinkage period. I have set out the average amounts of actual shrinkage in the several dimensions for the entire group of skulls. Each skull was first measured within twelve hours after it was taken from the macerator and at intervals of one week thereafter. The work had to be interrupted and this is the reason for the smaller number of skulls in the series after the fourth week. In each dimension the greatest reduction took place during the first week but shrinkage was by no means complete within that period; it continued with small fluctuations to about the end of the sixth week although the amount after the third week is negligible and one would be unwise in attempting to identify it with assurance upon individual skulls. Since it is not practicable to measure length and breadth to less than 0.5 mm. or height to less than 0.25 mm. it is plain that a very slight fluctuation may cause, on different occasions, a different reading to these fractions of a millimetre. This accounts for the occasional actual average increase in dimension recorded by the plus ( + ) sign. If shrinkage is practically negligible after the third week in ordinary room temperature it is plain that no shrinkage will take place after three weeks if the skull is subjected to a dry heat such as is experienced in this building in the Winter. Hence my previous contention that one month's drying is sufficient receives confirmation.

The detailed data of weekly shrinkage are not reproduced here for but little further information can be obtained from them than from the contents of Table II. The question of the relative humidity of the atmosphere however presents itself for consideration. No actual records of the temperature and humidity of the laboratory were taken during the period of drying but we had some weeks which were unusually hot and others in which the humidity was very great. The relation of the data to these atmospheric conditions is naturally confused since the several skulls were at quite different stages of drying but

careful study of the shrinkages suggests that drying is hastened by heat and delayed by humidity. In particular the week ending July 14 was excessively humid and among the records for that week there is an unusual feature in the number of actual increases of 0.5 mm. in the dimension. During the succeeding four weeks when no measurements were taken the skulls tended to shrink back to their dimensions of July 7, nearly all the increases proving to be temporary.

If the percentage of shrinkage be worked out for each week or for several weeks it will readily be seen that there is no constant relationship in the shrinkage. Some factors are at work which determine, for each skull, the rate of shrinkage in each dimension. Since the two halves of the skull fit throughout the shrinkage period it is further obvious that these factors, whatever they may be, act symmetrically. One should then inquire what may be the nature of these factors.

#### THE PROBLEM OF SHRINKAGE

Table I has already shown us that there is no real influence of sex or human Stock upon shrinkage. Small as the series in this investigation is the sex groups provide an effective brake upon any assumption of an aetiology related to Stock and likewise the Stock groups preclude any hypothesis regarding sex. That these features would have an influence upon bone shrinkage is, in any case, doubtful, for there is obviously one human type of bone and as an organic compound it is unlikely to differ with sex or Stock. The difference between Negro bone and White bone, so frequently assumed merely as a result of gross inspection, does not make itself obtrusive in the large collections of this laboratory.

Failing sex and Stock one would think of age, of cranial thickness and of patency of sutures as possibly being of some influence in this shrinkage.

We know that there are definite changes occurring in the texture and fundamental composition of bone at successive ages. The trend of these alterations in the case of the scapula has been outlined in a recent paper of great importance and suggestion by Graves (3). So far no other bone has been examined with the meticulous care necessary to discern the specific changes. But commencing in the ribs and vertebrae at about fifty years and spreading to other parts of the skeleton thereafter there is perceptible to touch and hearing a striking modification which denotes a significant change in bony composition. This will be described in detail in a later communication; it is sufficient at the moment merely to allude to it as the most fundamental of all the age changes in bone composition. Apart then from the question of suture closure we may examine the series for variations in shrinkage related to age. Table III gives a summary of these observations. In order to make any result more apparent I have set down the sum of the final measurements in length, breadth and height on the fully dried cranium, the total shrinkage of these three dimensions and the percentage of the latter upon the former. Column 6 shows that there is considerable variation in shrinkage but no real relationship to age.



Table III. *Total shrinkage in all dimensions.*

1	2	3	4	5	6	7	8
Skull	Age	Group	L. + B. + H. mm.	Total shrinkage	%	Cephalic index	Condition of cranium
897	32	Male	442.0	3.5	0.79	749	Medium
900	35	White	457.5	4.5	0.98	789	"
883	39		448.5	3.75	0.84	762	Thick
952	40		457.5	4.5	0.98	784	Thin
939	50		438.5	3.5	0.80	884	"
896	53		447.5	3.75	0.84	672	"
884	60		426.5	4.5	1.05	837	Medium
895	c. 60		458.5	5.0	1.09	731	Thick
912	63		461.25	4.75	1.03	867	"
903	67		433.0	4.0	0.92	775	Thin
905	77		460.5	3.75	0.81	782	Medium
724	31	Female	422.5	4.0	0.95	749	Thick
886	32	White	430.5	5.5	1.28	725	"
893	51		395.0	4.25	1.08	773	Medium
935	60		425.25	4.75	1.12	807	Thick
874	23	Male	443.0	6.0	1.35	783	Very thick
855	28	Negro	421.5	7.75	1.83	742	Thin
906	35		436.5	5.0	1.14	727	Thick
891	38		445.75	3.75	0.84	741	"
864	c. 48		448.0	6.5	1.45	767	Medium
911	58		430.5	5.75	1.34	708	"
954	24	Female	416.0	3.5	0.84	749	Medium
773	60	Negro	434.25	5.75	1.32	773	Thin
751	65		416.0	6.0	1.44	734	Very thick

Taking the averages of all specimens in each group we obtain the following figures:

Male White.	Average L. + B. + H.	448.2 mm.;	average shrinkage	4.14 mm., i.e. 0.92 per cent.
Female White.	"	"	418.3 mm.;	" " 4.62 mm., " 1.11 "
Male Negro.	"	"	437.5 mm.;	" " 5.79 mm., " 1.31 "
Female Negro.	"	"	422.1 mm.;	" " 5.08 mm., " 1.20 "

This gives a general average shrinkage of 1.13 per cent.

From these figures it appears that the average shrinkage for the cranium generally in Whites is about 1.0 per cent. of the final dimensions and for the Negro about 1.25 per cent. Whether there is any real significance in the evident Stock difference in these figures we cannot say; the groups are too small. To increase the size of the groups would be possible but the work is exacting and time-consuming. About two thousand measurements, including all check measurements, are embodied in the present investigation. Considering the individual differences it is extremely doubtful if this apparent Stock difference is real or would justify the great expenditure of time necessary for its thorough elucidation.

Thickness of the cranial bones might be invoked as a possible factor affecting the amount of shrinkage. An accurate estimate of thickness has yet to be worked out. Isserlis has asserted that there is no appreciable difference in thickness of the Negro skull as compared with that of the White(4), though this matter deserves further investigation. Meantime I have attached to Table III a general estimate of the relative thickness of the cranial bones

obtained by naked eye inspection and by palpation of the bisected cranium. A few moments' study of the records makes it clear that there is no definite relation of relative thickness either to age or to absolute or relative shrinkage.

Lest one should have some idea that perhaps shape of skull might influence shrinkage I have inserted in Table III a statement of the cephalic index of each specimen but a glance at this column serves to eliminate any such impression.

We now come to the question of suture closure and it will be remembered that Broca investigated this possibility upon a much more restricted sample and concluded that the state of the sutures is without influence (1, pp. 83, 85). It is a little difficult to set forth briefly and yet clearly the amount of closure in the several sutures. The whole question of suture closure is the subject of a memoir which, in association with D. W. Lyon, I am now preparing for publication. There is considerable individual variation in the extent of suture closure at any given age and this variation is much more marked on the external face of the cranium than on the inner surface. However, the effect of union at a suture as an agent which may conceivably influence shrinkage is not dependent upon the extent of union. If the adjacent bones are knit at a few discrete points they will be held together as firmly, from this point of view, as if the area of union were much more extensive. A detailed tabulation of the precise amount of union could therefore have no present significance and would be very confusing to the reader. In consequence I submit in Table IV merely a statement of the presence or absence of union at each suture, it being understood that if some union is indicated the amount of union is sufficient to maintain constant the relation of the apposed bones. The dimensions and actual shrinkage are expressed in millimetres, only those sutures being mentioned which conceivably might have some relation to shrinkage of the cranium as a whole. The plus (+) sign indicates some union, the cipher (0) absence of union.

On its face this table shows that the condition of the sutures can have no actual influence upon shrinkage. There is no skull in which all the sutures are patent and there are but five in which all sutures show some union, yet it is a simple matter to pick out test cases for shrinkage of any dimension. For example one might with reason expect that No. 906 would show more shrinkage both in length and breadth than No. 864 (both male Negroes) for it is not only from a younger individual but exhibits no closure in any suture except the sagittal whereas the latter has some union in all sutures. Nevertheless the shrinkage of No. 864 is 0.5 mm. greater in each direction. Coronal and Lambdoid sutures happen to present some union throughout the male White group yet the shrinkage in length varies all the way from 0.0 to 2.0 mm.

The lack of uniformity in shrinkage is well indicated by comparison of the two female Negro skulls 954 and 751. Both have the same total dimensions; the former is young and presents practically no union at the sutures, the latter is much older and shows considerable union. Yet the shrinkage in skull 751

Table IV.

Closure of sutures										Final dimensions in mm.					
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Skull	Age	Group	Sagittal	Coronal	Lambdoid	Squamous	Parieto-mastoid	Spheno-temporal	Masto-occipital	Length	Shrinkage	Breadth	Shrinkage	Height	Shrinkage
897	32	Male	+	+	+	+	+	0	+	187.5	1.0	139.5	1.5	115.0	1.0
900	35	White	+	+	+	0	0	0	+	190.0	1.5	149.5	1.5	118.0	1.5
883	39		+	+	+	+	+	+	+	189.0	0.0	142.5	2.0	117.0	1.75
952	40		+	+	+	0	0	0	0	189.5	1.5	149.0	1.0	119.0	2.0
939	50		+	+	+	0	0	0	+	170.0	2.0	151.5	1.0	117.0	0.5
896	53		+	+	+	0	+	0	+	200.5	1.5	135.0	0.5	112.0	1.75
884	60		+	+	+	0	0	+	+	172.5	1.0	143.5	2.0	110.5	1.5
895	c. 60		+	+	+	+	+	+	+	193.0	1.0	141.0	2.5	124.5	1.5
912	63		+	+	+	+	+	+	+	181.5	2.0	155.5	1.0	124.25	1.75
903	67		+	+	+	+	+	+	+	181.5	1.5	139.0	1.0	112.5	1.5
905	77		+	+	+	0	0	+	+	195.0	1.0	152.5	2.0	113.0	0.75
724	31	Female	+	+	0	0	0	0	+	179.5	0.5	133.5	2.0	109.5	1.5
886	32	White	0	+	0	0	0	0	+	182.0	1.0	132.0	2.0	116.5	2.5
893	51		+	+	+	0	0	0	+	162.0	2.0	125.5	1.0	107.5	1.25
935	60		+	+	+	+	+	0	+	173.0	1.5	139.5	2.5	112.75	0.75
874	23	Male	+	+	0	0	0	0	0	184.0	2.5	143.5	2.0	115.5	1.5
855	28	Negro	+	+	+	+	+	0	+	182.5	3.0	134.5	2.5	104.5	2.25
906	35		+	0	0	0	0	0	0	186.0	1.5	135.5	2.0	115.0	1.5
891	38		+	+	0	0	0	0	+	192.5	1.5	144.0	1.5	109.25	0.75
864	c. 48		+	+	+	+	+	+	+	189.0	2.0	144.0	2.5	115.0	2.0
911	58		+	+	+	0	0	+	+	188.5	2.5	134.5	2.0	107.5	1.25
954	24	Female	0	0	0	0	0	0	+	176.0	1.0	131.0	1.5	109.0	1.0
773	60	Negro	+	+	+	0	+	0	+	182.0	1.5	140.0	2.0	112.25	2.25
751	65		+	+	0	+	0	0	+	176.5	2.0	129.5	2.0	110.0	2.0

+ indicates some union; 0 indicates no union.



is actually almost double that in No. 954. This investigation therefore fully bears out Broca's conclusion based upon the estimation of capacity before, during and after soaking, namely that condition of the sutures is of no moment.

We have now examined the possible relation of all the factors usually called in as conceivable factors acting directly or indirectly on skeletal changes and are compelled to admit that not one of them can justly be invoked in the case of shrinkage. We are in fact reduced to the hypothesis of Broca at the conclusion of his investigation. "*Les propriétés hygrométriques des crânes sont très-variables, ce qui peut dépendre à la fois de la porosité de leur tissu et de l'état de leur matière organique.*" In other words we come back to the composition of bone itself, the study of which has not yet advanced far enough for us either to confirm or refute Broca's suggestion.

#### THE CHARACTERISTICS OF SHRINKAGE OF THE CRANIUM

Baffled as we are for the present in our effort to determine the really influential factors which define the precise percentage of shrinkage there are certain features of this shrinkage which deserve some passing emphasis.

In the first place the shrinkage in the several dimensions is roughly compensatory. If, as in No. 883 there is negligible shrinkage in one dimension there will be a maximal shrinkage in the other dimensions. Excessive shrinkage in one direction, as in No. 895 is balanced by merely moderate shrinkage in the other dimensions. No doubt this generalisation must not be strained too far for the Negro males 855 and 864 do not appear to share this characteristic. It is to be observed, however, that the Negro groups show a relatively greater shrinkage than do the Whites, probably an individual variation it is true, but nevertheless somewhat disconcerting. In these Negro samples the explanation may be that the figures for shrinkage in any dimension are not really excessive.

Secondly the shrinkage is symmetrical with a result that at all stages of the process the two halves of the bisected skull fit accurately and no warping occurs.

Thirdly there is a slight play of the portions of the skull upon one another in the process of shrinkage. This is most readily studied in the breadth measurement. It results in a shifting of the site of greatest breadth during drying, the distance of the shift being out of all proportion to the difference in breadth which at its maximum amounts merely to a fraction of a millimetre. This shift with the relative stage at which it took place during drying is exhibited in Table V. Once again we have a feature of drying which presents no relation whatever to the state of the sutures reasonably presumed to possess some influence.

The first site mentioned is that of greatest breadth on the first measuring after emergence from the macerator. The number of weeks denotes the date of measurement after emergence from the macerator when the particular site became the Euryon. The last site mentioned is the permanent site of greatest breadth. Between the middle of July and the middle of August no measure-

Table V. *Site of greatest breadth during drying.*

Skull	Group	Condition of sutures		Site of greatest breadth with dates of change (weeks of drying)
		Squamous	Parieto-mastoid	
897	Male	+	+	<i>ss.</i> ; no change
900	White	0	0	<i>tp.</i> ; <i>ss.</i> 1 week; <i>tp.</i> 3 weeks
883		+	+	<i>pi.</i> ; no change
952		0	0	<i>pi.</i> ; „
939		0	0	<i>ss.</i> ; „
896		0	+	<i>pi.</i> ; <i>ss.</i> 1 week
884		0	0	<i>ss.</i> ; <i>pi.</i> 2 weeks; <i>ss.</i> 3 weeks; <i>pi.</i> 7 weeks
895		+	+	<i>ss.</i> ; no change
912		+	+	<i>ss.</i> ; „
903		+	+	<i>ss.</i> ; <i>pi.</i> 3 weeks
905		0	0	<i>ss.</i> ; no change
724	Female	0	0	<i>ts.</i> ; „
886	White	0	0	<i>pi.</i> ; „
893		0	0	<i>pt.</i> ; „
935		+	+	<i>ss.</i> ; <i>tp.</i> 1 week
874	Male	0	0	<i>pm.</i> ; <i>pi.</i> 7 weeks
855	Negro	+	+	<i>pi.</i> ; no change
906		0	0	<i>ss.</i> ; <i>ts.</i> 5 weeks
891		0	0	<i>ss.</i> ; <i>ts.</i> 3 weeks; <i>ss.</i> 6 weeks; <i>ts.</i> 7-11 weeks
864		+	+	<i>ss.</i> ; <i>pi.</i> 2 weeks; <i>ss.</i> 3 weeks; <i>pt.</i> 9-13 weeks
911		0	0	<i>ss.</i> ; no change
954	Female	0	0	<i>pt.</i> ; „
773	Negro	0	+	<i>ptss.</i> ; <i>pt.</i> 1 week; <i>ptpm.</i> 3 weeks; <i>pt.</i> 4 weeks; <i>ptpm.</i> 5 weeks
751		+	0	<i>pi.</i> ; no change

As in Table IV the plus (+) sign indicates some union of the suture, 0 denotes absence of union. The site of the Euryon or point of greatest lateral projection of the cranium is indicated by letters in the manner suggested by Martin<sup>(6)</sup>.

1. *pt.* Greatest breadth at the parietal eminences.
2. *pm.* „ „ midway between 1 and 4.
3. *pi.* „ „ at the lowest part of the parietal bone.
4. *ss.* „ „ at or immediately adjacent to the squamous suture.
5. *ts.* „ „ in the upper part of the squamous temporal.
6. *tp.* „ „ in the posterior part of the squamous temporal.

ments were taken; hence if a change took place during this period it cannot be defined more precisely than is done in the cases of Nos. 864 and 891. Occasionally, as in No. 773, there were two sites where the breadth was equal and greatest; these are indicated by a combination of the letters above tabulated. Of the sutures which might be suspected of influencing this measurement the condition of the squamous and parieto-mastoid alone are indicated. The sagittal which might have some remote effect, showed some union in all except Nos. 886 and 954.

From a glance at the table it is perfectly obvious that there is no effect whatever upon the stability of the Euryon ensuing from the condition of the sutures listed. Where the sutures are completely patent there may be no change in site of the Euryon during drying; even where union of the sutures precludes any actual movement of the articulating bones there may occur

quite marked and frequent fluctuations in site. No. 864 seems specially significant in this respect for its squamous sutures were four-fifths united and the parieto-mastoids completely closed, at least upon the inner cranial face. The individual variation in site of the Euryon is of no consequence. The astonishing thing is the change in its position which occurs in so many skulls, and that without any apparent strain in the skull or any resultant warping. This absence of warping in properly macerated skulls in contradistinction to that found in exhumed specimens was specially noted by Broca. Actual drying in a normal atmosphere continues over many weeks before the dimensions finally steady and the change in position of the Euryon may occur three months after the skull is taken from the macerator.

#### COMPARISON OF CRANIAL SHRINKAGE WITH THAT IN OTHER BONES

One would naturally inquire whether this shrinkage is uniform throughout the skeleton so that one might allow a certain percentage for shrinkage on any bone, whatever its shape. In the skull this amount would average 1.1 per cent. of the final dimension. Towards the solution of this problem we have as yet no direct evidence to go upon. In a forthcoming extensive monograph on the femur my colleague Dr Ingalls proposes to set forth the facts for that bone but until the study is completed we can only make certain inferences from data not directly apposite.

Pearson has devoted some attention to the question in the case of the femur and gives noteworthy conclusions (7, pp. 193, 194, 244). Many years ago Welcker soaked one male femur for three days and found it to increase 1.2 mm. in length. In 1873 Broca took three femora and soaked them for seven days. Of these three bones one had just been macerated that same year, one was from the fifteenth century and one was neolithic. The extension upon soaking measured 1.5 mm., 1.5 mm., and 1.0 mm. respectively. Pearson repeated the soaking experiment with one each of the femur, tibia, humerus and radius taken from burials between two and three hundred years old. After soaking for five days the measurements were contrasted with those of the bones when first received, due control measurements being used. To these notes were later added observations upon two Naqada femora soaked for five and six days respectively. The measurement in each case was the greatest length (excluding spine in tibia), for the femur the oblique length being used. It might be well to comment that this includes an angle and that the trochanteric length might give a more reliable criterion. The results obtained permit the following tabulation.

Femur 1 (Naqada).	Dry 408.0 mm.; shrinkage 2.4 mm.; i.e. 0.59 per cent.
Femur 2 (Naqada).	" 443.1 " " 2.2 " " 0.50 "
Femur.	" 425.8 " " 2.6 " " 0.61 "
Tibia.	" 374.1 " " 1.7 " " 0.45 "
Humerus.	" 345.2 " " 1.3 " " 0.38 "
Radius.	" 231.1 " " 0.7 " " 0.30 "



There is in these figures a considerable individual variation and, for the femur, they are about twice as great as those of Broca and Welcker. This perhaps may be due to the difficulty experienced by the latter workers in measuring so small a difference in length. The figures cannot be directly compared with mine on the skull but one should note that the greatest percentage increase is slightly more than twice the smallest. Now the individual variation in shrinkage of combined skull measurements in my series is from 0.79 per cent. to 1.83 per cent., or taking the maximum of the male Negroes alone, from 0.84 per cent. to 1.83 per cent. From these figures it is obvious that the extent of the shrinkage covers a considerable range. The great individual variations in shrinkage may conceivably be attributed to the differences in structure of the different parts of the same bone. Difficult though it may be, I do not think, however, that these variations entirely preclude an attempt at estimating a percentage allowance for shrinkage. Such an objective must indeed be attained if we are to make a real effort at the approximate estimation of shrinkage in bones like the vertebrae where actual shrinkage could scarcely be measured. However, individual differences make any assumptions regarding this matter unprofitable at the moment. There is one observation, however, which makes one hesitate to apply the use of the 1.1 per cent. shrinkage of the skull to any long bone. This is the fact that, by subtracting only 2.6 mm. for shrinkage in the case of the femur and 1.3 mm. for the humerus, Pearson was able to convert the measurements of Rollet on Dissecting Room bones approximately into those of Rahon for dry macerated bones (7, p. 195). Too much weight, however, must not be laid upon this agreement for it may be merely an accident of random sampling. Random sampling from a single series may result in a difference just as striking as is this agreement between samples of different series. For example Dr Ingalls informs me that the mean oblique length of the right femur of 100 male White skeletons in our collection is 457.8 mm., but in addition he tells me that in a second random sample from the same series consisting of 99 right femora the mean is 455.3 mm. and in yet another series which comprises both the foregoing and includes others to the total of 217 the average oblique length is 452.8 mm. At this point then the discussion must be left for the present, pending direct data upon the shrinkage of the long bones themselves.

#### COMPARISON OF DIMENSIONS IN THE WET MACERATED SKULL WITH THOSE OF THE SAME SKULL GREEN

The crux of this whole investigation is summed up in the question as to how far the dimensions of the wet macerated skull present those of the same skull green, that is to say, before maceration but after the soft parts including the periosteum have been cut away. It is essential to become acquainted with this relation since, with our knowledge of the shrinkage of the skull in drying, and our estimate of the thickness of the soft overlying tissues, it will enable

us readily to reconstruct the dimensions of the living head from those of the dry skull and *vice versa*.

There are only eight of the twenty-four skulls used as the basis for this work which were measured in the green condition upon the apparatus described in the earlier part of the communication. Taking the eight skulls I find the following average differences in dimensions when measured first in the green state and secondly within twelve hours after emergence from the macerator.

Length 0.25 mm. Breadth 0.37 mm. Auricular height 0.22 mm.

If the reader refers to my former communication(8) he will find that the possible instrumental errors, as worked out for the instruments used in these measurements, are:

Length 0.2 mm. Breadth 0.3 mm. Auricular height 0.2 mm.

In view of these latter figures it may seem absurd to base any significance upon the differences recorded immediately above. But, it may be asked, why have I not made this instrumental correction throughout? The reply is that the instrumental error is used in cases where one has reason to suspect that the conditions of the work do not permit it to be ignored. In the present investigation where very small differences were expected and the most painstaking efforts were made by instrumental standardisation and repeated check measurements to attain the greatest accuracy possible I do not consider that the small instrumental error need receive any consideration. But this elimination of possible instrumental errors itself demands that the average alteration in dimensions consequent upon change from the green to the wet macerated condition be not ignored. We are dealing with a very delicate series of measurements and although an error such as would be incurred by leaving out of account a total difference of 0.84 mm. change in dimension may seem small, yet it is quite enough to upset seriously the probable exactitude of our estimation of change in capacity. Consequently it is necessary to combine this difference between the green and wet macerated dimensions with the reduction already found to occur during drying and recorded in row 5 of Table I. The total average reduction in dimensions will now be:

Length 1.77 mm. Breadth 2.10 mm. Auricular height 1.72 mm.

For purposes of computation these figures can be simplified to

Length 1.8 mm. Breadth 2.1 mm. Height 1.7 mm. Total 5.6 mm.  
and will be so used in the succeeding argument.

Eight skulls nevertheless is a very small number upon which to base an estimate of the difference between the wet macerated skull and the green skull. The macerated skulls were first measured some hours after removal from the macerator and a small amount of shrinkage might be suspected of having already taken place. Pearson indeed feared that such occurred in Broca's series, but Warren did not measure the two Naqada femora until eight or nine hours after extraction from the water bath and Pearson notes that the maximum rate of

contraction in a normal atmosphere is not reached before the second or third day. In order to check my estimate I have reproduced as row 6 in Table I the results of my preliminary examination (see (8), Table X), the skulls in which were first measured in the green state and again later after several weeks of drying. I have also remeasured these same ten skulls of row 6 after three months more and presented the results as row 7. Lastly I have taken another ten male White skulls likewise first measured in the green state and then wet after being macerated and have inserted the results of that group as row 8. Rows 6, 7, 8 all refer to skulls measured with the old apparatus (see (8)) from which the instrumental errors have necessarily been deducted. Having regard to the individual variation in shrinkage which has been shown to exist and considering the data given in the several columns of Table I, I am convinced that there is a real though small difference between the dimensions of the green skull and those of the same skull when macerated and still wet, but that this difference may be accounted for by a small shrinkage occurring in the first few hours of drying.

The conclusion just set forth must not be taken to mean that there is necessarily no transformation taking place in the bone substance during maceration. It merely denotes that actual change in dimensions occurring as a result of the loss of organic material in maceration must be very small. The further question which presents itself is why my results always show a greater difference between the wet and the dry bone, sometimes a much greater difference, than those of previous investigators. The answer is that a bone, when immersed in water after being dried, never really reaches the dimensions which it had in the green or living condition. I do not think that it is correct to argue from the dry bone to the wet one in order to obtain a true approximation to living dimensions. The only method which can inspire entire confidence is one involving the reverse process and for this reason I believe the results now obtained are more dependable than those of earlier workers.

Having outlined this conclusion it is necessary to review the work which I have previously done upon the alteration in capacity consequent upon drying of the skull. The average reduction in capacity I have shown to amount to about 50 c.c. This has been demonstrated both by direct measurements and indirectly by calculation from change in dimensions. By the direct method the average reduction in capacity of three skulls was 60 c.c. This is unexpectedly large and in consequence of the difficulties in the technique, may indeed be too great. It seems at least very suggestive that the only one of the three which was absolutely water-tight showed a reduction of only 49.5 c.c. I had been inclined to consider this as far the most accurate result, coming as it does within the range allowed by Broca. But later work and the demonstration of considerable individual variation render these deductions unwarrantable. By computation from my preliminary observations on change in dimensions I arrived at the conclusion that an average skull of about 1500 c.c. would diminish in capacity during drying about 47 c.c. It is at this point that my



former investigation ceased for lack of sufficient observations. The reduction in dimensions in transformation from the green to the dry macerated state called for in my earlier communication was the following:

Length 2.3 mm. Breadth 2.25 mm. Auricular height 1.8 mm.

These were deduced from the measurements of ten male White skulls. From the present study we find that these figures must be somewhat reduced to permit a more comprehensive generalisation. Now the type skull used previously was No. 878, a male White. Using Lee and Pearson's mean reconstruction formula No. 9(5) with the dimensions of this skull in the green state we calculate its capacity thus:

$$\cdot 000337 \times 183 \times 149.5 \times 120.5 + 406.01 \text{ i.e. } 1517 \text{ c.c.}$$

Making the necessary corrections for shrinkage we have:

$$\cdot 000337 \times 181.2 \times 147.4 \times 118.8 + 406.01 \text{ i.e. } 1475 \text{ c.c.}$$

hence the reduction in capacity is computed at 42 c.c. Again this comes within the range defined by Broca and the reduction in capacity is only 5 c.c. less than I obtained in my preliminary work. This is very satisfactory and, I believe, puts the problem of skull shrinkage into such a condition that deductions made may be relied upon. In conclusion one may profitably compare the results obtained from this rather intensive study aided by instruments of precision with results just as carefully made but with less improved instruments, making allowance for the instrumental error of the latter. Taking the average shrinkage of the three sets of observations with the "old instruments" (see (8)) set forth in rows 6, 7, 8 of Table I we find:

Length 1.78 mm. Breadth 2.02 mm. Auricular height 1.97 mm.

a combined total of 5.77 mm. which is remarkably close to the revised and final sum of 5.6 mm. which I propose to adopt as the result of the present study. The tentative total of my former work which may now be discarded was 6.35 mm., but this of course was based upon a very restricted sample.

#### COMPUTATION OF SHRINKAGE IN VOLUME FROM CHANGE IN LINEAR DIMENSIONS

In the foregoing section I have discussed the average shrinkage as obtained directly and by computation, but to complete this study it is necessary to ascertain with what confidence the shrinkage in capacity may be calculated upon individual skulls of which one knows the change in dimensions consequent on drying. As a guide to the dependability which one may expect in this matter I have obtained the cranial capacity in the dried state of skulls 952 and 954 which served as natural *crânes étalons* in my earlier work (8). Reference to that paper will show the estimates of capacity for these skulls, with the skull intact, when the skull is bisected but with the membranes *in situ*, and finally after removal of the membranes; each estimate being the mean of seven determinations. To obtain an estimate of the capacity by the water method after thorough drying for four months I treated the skulls with cellu-

loid varnish and plasticine as already described (8), again taking the mean of seven determinations. My results are the following:

*Skull 952, male White, German, age 40 years.*

Capacity of green skull bisected, membranes removed	1646.5 c.c.
Capacity of dried skull bisected	1615.6 „
Shrinkage in volume directly determined	30.9 „

*Skull 954, female Negro, age 24 years.*

Capacity of green skull bisected, membranes removed	1173.4 c.c.
Capacity of dried skull bisected	1145.7 „
Shrinkage in volume directly determined	27.7 „

Our records of these skulls give the following dimensions in millimetres.

*Skull 952.*

Green measurements: Length	190.5	Breadth	151.0	Auricular height	120.5
Dried „ „	189.5	„	149.0	„	119.0

*Skull 954.*

Green measurements: Length	177.0	Breadth	132.0	Auricular height	110.5
Dried „ „	176.0	„	131.0	„	109.5

In each case the linear dimensions were measured again after the capacity determinations had been carried out on the dried skull in order to insure that the technique had not caused the measurements to increase. I was particularly anxious to be sure of this since there is such a great individual variation in shrinkage. Having satisfied myself that all measurements and estimates were as accurate as possible I next calculated the capacity from the green and dry dimensions. It is of no significance whether one adopts a local formula or one of those computed by Lee and Pearson (5), for we are not now concerned with the relative accuracy of capacity. The calculation of shrinkage is entirely independent of the accuracy in calculation of actual capacity. As a matter of fact one would expect that Lee and Pearson's formula should give a closer approximation to the actual capacity than our own formula, since the latter was computed for giving the capacity of the green skull from the dimensions of the dry. At any rate this problem has already been fully inquired into (8). No formula involving the auricular height has yet been worked out for female Negro skulls nor have we any local formula for females. The formulae used are three:

(1) W. R. U. male White formula 5.  $\text{Cap.} = 5.119 \text{ L.} + 7.357 \text{ B.} + 9.539 \text{ H.} - 1709.49.$

(2) L. and P. reconstructed male White formula 9.  $\text{Cap.} = .000337 \times \text{L.} \times \text{B.} \times \text{H.} + 406.01.$

(3) L. and P. „ female „ „ 9.  $\text{Cap.} = .000400 \times \text{L.} \times \text{B.} \times \text{H.} + 206.60$

Now skull 952 upon calculation by formula (1) has a green capacity of 1526.0 c.c. and a dry capacity of 1491.9 c.c. This gives a shrinkage of 34.1 c.c. By the use of formula (2) the green capacity is 1538.3 c.c. and the dry capacity is 1574.1 c.c., resulting in a shrinkage of 35.8 c.c. Since the actual measured shrinkage is 30.9 c.c. either of the two mathematical methods gives a result almost if not quite as dependable as direct determination.

Skull 954 by method (3) above, gives a green capacity of 1239.3 c.c. and

a dry capacity of 1211.8 c.c. The difference between these, namely 27.5 c.c., is the calculated shrinkage, a figure almost identical with the 27.7 c.c. obtained by direct determination.

The unexpected success of these calculations decided me to make a trial of the method upon the three skulls of Table IV in my former work (8). These skulls were measured green and dry on the old apparatus and the capacity determined in the green condition with membranes *in situ* and later in the dry macerated condition. The green capacity after removal of membranes was not taken in these skulls; consequently this figure must be approximated by the addition of 50 c.c. (the mean dura volume, see (8)). Subtraction of the dry capacity from the figure now obtained will give an approximation of the actual shrinkage. In this way the "actual" shrinkage for male White skulls 878, 865, 856 is found to be 61.0 c.c., 68.9 c.c. and 49.5 c.c. respectively. Using formula (1) the respective calculated shrinkages are 63.4 c.c., 69.7 c.c. and 71.2 c.c. For skulls 878 and 865 the results again are surprisingly close, but this closeness is an accident, for the true volume of the dura of these skulls is not known. Moreover it is certain that there is great variation in dura volume. By mere accident these figures are almost as close as those for skulls 952 and 954 in which the closeness of the direct and calculated determinations is due to accuracy of data. Nevertheless it does show how reliable the calculated figure for shrinkage may be.

Skull 856 is somewhat different and is most important. There was absolutely no leak at all from this during the determination of capacity after drying; I do not believe that the few drops escaping from the other two really modify the accuracy of the results in their case but in this one there could be no question. Now whereas the shrinkage calculated from the green and dry linear dimensions is 71.2 c.c., that obtained directly, upon the assumption that the dura volume is the average amount of 50.0 c.c., is only 49.5 c.c. Presuming, as we have a right to do, from the results just announced, that mathematical calculation gives a close approximation to the truth, the discrepancy here of 21.7 c.c. may be due to an error in determination of the actual capacity under different conditions, to an error in the original determination of the green linear dimensions or to an unusually voluminous dura. It cannot be accounted for by an error in determination of the linear dry dimensions for I have repeated these and find them correct. It certainly is not due to error in the direct measurement of dry capacity for there were no leaks and the estimate is the mean of five determinations. It might be found in the original direct measurement of green capacity which is the mean of only two determinations. But the difference between these two determinations amounts merely to 15 c.c. and our experience shows that with so small a difference the mean can be depended upon as a fair approximation to the true value. We are left then with the alternatives of erroneous linear measurements of the green dimensions on the one hand, measurements which obviously cannot be reviewed, and an unusually voluminous dura on the other. The dura volume was not determined directly



in this case but even if the whole discrepancy of 21.7 c.c. were added to the mean volume of 50.0 c.c. the result would not be a startling instance of individual variation. Nevertheless I am more inclined to believe that the green dimensions are somewhat too large. A shrinkage of 4.0 mm., 3.0 mm. and 3.0 mm. respectively in length, breadth and auricular height is too large to be accepted without comment. Moreover the skull is asymmetrical, a condition which always rendered the measurement of length and to a less extent of breadth, by the old apparatus, rather difficult. Granted then that the error has been run to earth in the last category this skull stands as an exception which emphasises the reliability in general of the mathematical calculation of shrinkage as shown in the case of the other four.

#### SUMMARY

1. Shrinkage of the several dimensions of the cranium consequent upon transformation from the green to the dry macerated state bears no constant relation to the particular dimension. Great individual variation occurs and the percentage shrinkage, relatively small for length, increases somewhat for breadth and auricular height. On the average of all dimensions the shrinkage amounts to about 1.1 per cent. of the final dried measurement.

2. The duration of measurable shrinkage in a normal summer atmosphere is about three weeks. Shrinkage certainly continues beyond this time but it is most clearly demonstrable by a shifting of the Euryon, fluctuation of the location of which may continue for three months. Shrinkage is naturally greatest during the first week of drying. Changes in temperature and humidity do affect the reduction temporarily and may even result in slight fleeting increases in dimension.

3. Of the factors which might be invoked as influencing shrinkage directly or indirectly we are able to eliminate sex, Stock, age, cranial thickness, cranial shape and condition of sutures.

4. Of the characteristics of shrinkage three stand out fairly plainly. Shrinkage in the several dimensions is roughly compensatory. It is symmetrical. There is an actual play of the bones (or of the parts of bones) the one upon another during shrinkage, a play which is shown by the shifting in position of the Euryon, does not result in warping, and is independent of the condition of the sutures.

5. At the moment we have no data upon other bones which may be used for comparison with cranial shrinkage but this defect will presently be remedied.

6. In passing through the stage of maceration and during the first few hours thereafter the green skull loses a total average of 0.84 mm. in length, breadth and auricular height. This loss probably occurs during the first few hours of drying.

7. The average reduction in dimensions in transformation from the green to the dry macerated condition is the following:

Length 1.8 mm. Breadth 2.1 mm. Auricular height 1.7 mm. Total 5.6 mm.

8. This shrinkage corresponds to a reduction of about 42 c.c. in a cranium of some 1500 c.c. capacity.

9. Given the linear dimensions in green and dry macerated states it is possible to calculate the shrinkage in capacity and the result will be accurate within a very few cubic centimetres, any discrepancy being due to variation in the dura volume. Further the accuracy of calculation of shrinkage is independent of the accuracy in calculation of actual capacity.

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## DUODENAL DIVERTICULA

By J. C. BORLEAU GRANT

THE last case of duodenal diverticulum recorded in this *Journal* was one by Jackson in the year 1908. Since then a number of articles dealing with the various aspects of the subject have been published especially in the medical and surgical periodicals. In 1910 Keith(1) was able to trace 14 specimens of this condition in the various museums of the medical schools in London, and in the following year Baldwin(2) published a *résumé* of all the cases recorded in the literature dating back to Morgagni. These numbered 67 in all. The condition was therefore regarded as a rare one.

The more systematic and everyday use of the X-ray and bismuth meal in the examination of gastro-intestinal ailments has been largely responsible for bringing the subject into prominence. For example, the independent findings of three observers(3,4,5) on over 10,000 patients examined in this manner are that from 1 per cent. to 1·2 per cent. of them had duodenal diverticula. Others working independently in the postmortem room(6,7) have discovered these diverticula in 3 per cent. of about 1500 bodies, while another(2) found that of 104 cadavera 14, that is 5·7 per cent., had duodenal diverticula. They can therefore no longer be regarded as rarities. In fact, these figures suggest that their occurrence is as frequent as is that of Meckel's diverticulum. Though both are liable at times to come within the sphere of the surgeon they belong primarily to that of the anatomist.

The following points are fairly well established:

The majority are small, ranging from 0·5 to 3·0 cm. in length. They have been described in the new born, but almost all occur in the later decades of life.

An attractive explanation as to their formation is put forward by Lewis and Thyng(8,9) who suggest that the transient intestinal pockets found by them so constantly in young embryos may develop into diverticula, that is that they are congenital; by most observers, however, they are regarded as acquired.

Such diverticula may possess all the coats of the normal gut, or, as is much more frequently the case, the muscle coat is missing or is at most represented by a few scattered muscle fibres.

The great majority are to be found attached to the concave, pancreatic aspect of the duodenum, and being obscured by the pancreas, are apt to remain undetected.

Most of them spring from the second part, commonly near or along the track of the common bile and pancreatic ducts; some, like similar protrusions



from other segments of the intestinal canal, are herniated along the path of a blood vessel, as has been excellently demonstrated (1,10), whereas others bear no such definite relation. For example, of 140 cases recorded by four observers (2,11,4,3), 23 were in the first part, 84 in the second, and 33 in the third.

Usually they are to be found singly, but in the proportion of 1 in 10, or thereabouts, two or more are met with: of 129 persons in whom three observers (3,11,2) detected diverticula 11 had two or more.

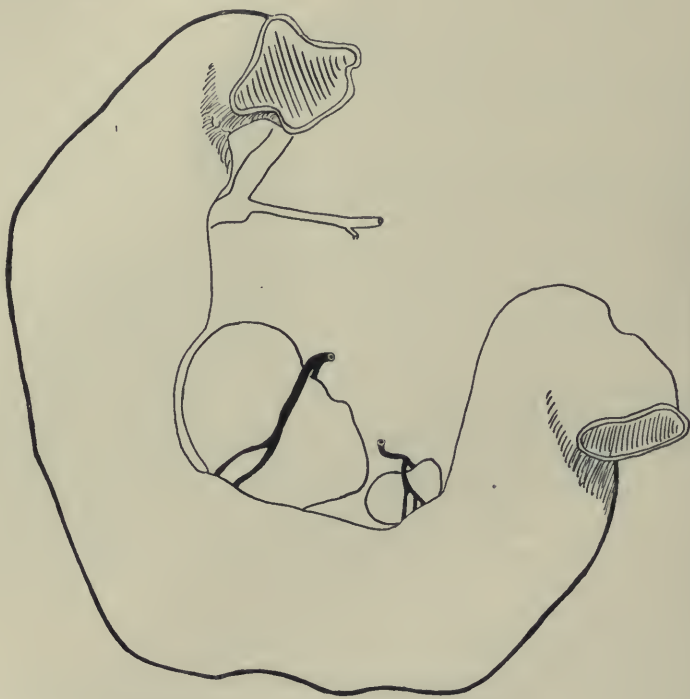


Fig. 1. Outline of Duodenum and Diverticula.

The specimen which is the subject of this note was found in the dissecting room. It has two sacs, a large and a small. The large resembles very closely in shape, size, and in position the one described by Jackson (12) in this *Journal* and depicted also in Keibel and Mall's *Embryology* (9). It is, however, slightly larger, its diameters being  $4.2 \times 3.3 \times 1.8$  cm. Being 5.0 cm. in circumference one can easily pass a finger through its mouth (it has no neck) into its large ovoid sac: the smaller, in every respect a miniature of the large, is 1.7 cm. long, and its orifice admits the stem of a pencil 2.2 cm. in circumference. The larger is 6.0 cm. and the smaller 10.0 cm. distal to the orifice of the conjoint bile and pancreatic ducts. Both sacs protrude between the same fasciculi of longitudinal muscle fibres of the gut wall as those between which the conjoint bile and pancreatic ducts pass. Further, an injected artery bifurcates at the fundus of each sac and as it were sits astride it, one branch passing on the

anterior aspect, the other on the posterior to the mouth of the sac. The impression given is that a hernia of the mucosa and of the submucous coat has taken place at the point of bifurcation of a vessel and that it has carried the bifurcation before it through the muscle wall. Sections of the sac stained with Van Gieson's stain show villi, and a hypertrophied muscularis mucosae well mixed with connective tissue fibres and, as can be seen microscopically, a muscular coat is absent.

Among other large sacs which have been described are those of Jackson (12) which measured  $3.5 \times 3.0 \times 2.0$  cm. and of Baldwin (2)  $6.0 \times 4.0 \times 2.0$  cm. Both of these like that herewith described had been treated with formalin. Case (3) estimates that a number of his cases when "barium filled" and X-rayed were 4.0 cm. long, and one which he removed by operation was 5.0 cm. in length. Downes (13) removed one measuring  $4.0 \times 3.5 \times 3.0$  cm. which like that of Case was evidently measured when fresh.

As this specimen had been laid aside with others before the abnormalities were noticed, it is not possible to state the age or sex.

I record the case as it may serve to remind those working in dissecting rooms of the condition.

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# UNMYELINATED NERVE FIBRES OF THE DORSAL ROOT

By W. F. WINDLE,

*Contribution No. 105 from the Anatomical Laboratory  
of the North-western University Medical School.*

AFTER cutting the second cervical nerve in the white rat, Ranson(1) found that nearly all of the cells in the corresponding spinal ganglion suffered chromatolysis. This occurred in spite of the fact that not more than one-third of the spinal ganglion cells are associated with afferent myelinated fibres in the nerve. Careful counts had previously shown that in this nerve there are almost exactly three cells in the ganglion for every myelinated sensory fibre in the nerve(2,3,4). The small cells, which are about twice as numerous as the large, and which had previously been assumed to be anaxonic(5), are those which show the greatest degree of chromatolysis. On the basis of this evidence, Ranson concluded that the small cells were probably associated with unmyelinated fibres in the nerve.

Both Cajal(6) and Dogiel(7) observed that the small cells of the spinal ganglia give rise to unmyelinated axones which divide dichotomously, sending one branch peripherally and one centrally. Ranson(8) confirmed these observations. He followed the fibres, after they divide, into the peripheral nerves for long distances, and into the dorsal roots for a very short distance. He was unable to trace them far into the dorsal roots because the pyradine silver method, which was used, does not give results with such small bundles of fibres as those into which the roots divide. However, he was able to see these fibres again as the dorsal roots enter the cord, where they can be followed into the tract of Lissauer(9). These unmyelinated fibres of the tract of Lissauer degenerate after sectioning the dorsal roots proximally to the spinal ganglion(10).

Miss Parsons(11), using the pyradine silver method and acid fuchsin connective tissue stain, suggested that these fibres were those of neuroglia. They did not stain with the connective tissue stain. She found them inconstantly distributed in different roots and in different parts of the same root. She also found similarities between these fibres and those brought out by using the same methods on tissues which are supposed to be composed almost exclusively of neuroglia. Miss Wilson(12) applied the differential neuroglia stains to the dorsal roots and spinal ganglia and found no neuroglia. She also pointed out that no neuroglia had ever been recorded by observers who used the Golgi method on these ganglia.

The small unmyelinated fibres of the vagus nerve, which appear as fine



black threads, when stained by the pyradine silver method(13), are identical in structure and stainability with these fine fibres of the dorsal roots. Although mechanical difficulties in staining the dorsal roots prevented Ranson from seeing the fine unmyelinated fibres except as they enter the roots from the ganglia and as they enter the cord from the roots, he felt justified in assuming their presence in the intervening portion. However, their presence here has recently been called into question(14), and so it seemed advisable to make a special effort to demonstrate them in this intervening portion of the dorsal root.

#### METHOD

Material was taken from the seventh lumbar nerves of large adult dogs. The whole dorsal root was divided into three equal segments. In one case the middle segment, and in another case the central segment was fixed in osmic acid. The remaining portions were prepared for the pyradine silver technique.

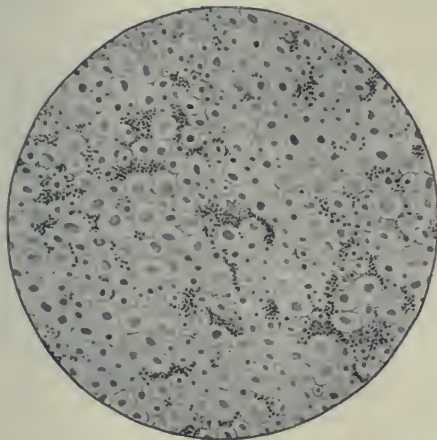


Fig. 1. Pyradinesilver preparation of the seventh lumbar dorsal root of a dog about 15 mm. from the cord. Drawing from tracing made with the Edinger projection apparatus. Magnification 310.

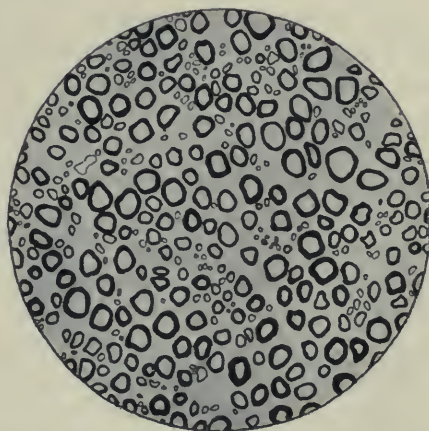


Fig. 2. Osmic acid preparation of the seventh lumbar dorsal root of a dog about 15 mm. from the cord. Tracing made with the Edinger projection apparatus. Magnification 310.

The pieces of nerve root were threaded into strips of spinal cord(15) and tied out straight upon a glass slide, although not stretched. Imbedding the pieces in spinal cord gave sufficient bulk for satisfactory silver impregnation to take place. The tissue was fixed in ammoniated alcohol and subsequently run through the process as described by Ranson in 1911(16). Excellent results were thus obtained.

#### RESULTS

The measurements of the myelinated fibres as given by Langley(14) are confirmed in the osmic acid preparations. The smallest fibres varied between two and three micra in diameter. Rarely a pale dot is seen and this might be interpreted as representing an unmyelinated fibre.

There is considerable shrinkage in the material prepared by the pyradine silver method as may be seen by comparing the two accompanying figures. The greatest amount of shrinkage occurs in the connective tissue among the fibres. A space is usually found between the very pale myelin sheath and the brownish yellow axon. This is due, no doubt, to a shrinkage in both axon and sheath. It is constant, however, and cannot be eliminated when this technique is used. The complete diameters of the myelinated fibres do not differ greatly from those of the myelinated fibres treated with osmic acid. They may be divided into the same three classes according to their diameters (14).

The unmyelinated fibres are usually seen in bundles, sometimes singly, running through the connective tissue among the myelinated fibres. They appear as small black dots when cut transversely, but the best conception of them is obtained from sections cut obliquely. Here they appear as fine threads running through the thickness of the section as the microscope is focussed up and down. Longitudinal sections show them as bundles of parallel black threads pursuing a somewhat wavy course among the myelinated fibres. They can be traced for long distances through the dorsal root and have never been seen to branch. Both drawings were taken from sections of dorsal roots approximately 15 mm. from the spinal cord, and an even greater distance from the spinal ganglia. As can readily be seen, the unmyelinated fibres are present in greater numbers than the myelinated ones. They are packed very closely together in the connective tissue but the individual fibres can be differentiated easily in thin sections by using an oil immersion lens. A few of the larger fibres are found to be somewhat over a micron in diameter, but the great majority of them measure one micron or less. Some are even less than a half micron in diameter. These diameters may be actually somewhat small since there is undoubtedly some shrinkage in the axon.

The question of the presence of these unmyelinated fibres in the dorsal roots is of considerable physiological importance because there is good evidence that they mediate painful afferent impulses (17). Since they fulfil in every way the requirements of Head's protopathic system their demonstration must be regarded as additional evidence in favour of his classification of sensory fibres. It is not improbable that the afferent myelinated and unmyelinated fibres correspond to the epicritic and protopathic fibres respectively (18).

I am indebted to Dr Ranson for calling my attention to this problem, and wish to thank him for his assistance during the work.

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## A SIMPLE AND RAPID METHOD OF MICROPHOTOGRAPHY

By DAVID WATERSTON.

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THE writer has long felt the need of a rapid and simple method of microphotography as a substitute for drawing by hand in connection with the study and reconstruction of serial sections of embryos.

There can be no question of the value of microphotographs in such work over drawings, but the time and the expense involved in preparing a number of such photographs, each of large size, on glass plates or films, and taking prints of each have formed very serious drawbacks.

The time and the cost involved can be very greatly reduced by taking the microphotograph directly on to sensitive paper. Such photographs appear as negatives, but this involves no disadvantage, as detail is as easily recognisable in the negative as in the positive print. Only one copy of each photograph is available, but this also implies no real drawback, for it is as easy and rapid to take a second photograph as it would be to take a print from a negative.

W. His indicates a method of this kind, in which he used a Bromide silver paper.

The wide range of photographic printing papers now available suggested to me that a paper might be found which was more easily handled and more adaptable than bromide paper.

After a series of trials, gaslight printing papers were found to serve the purpose admirably, and are obtainable in almost any size required.

The writer uses for preference Illingworth "Slogas" paper, vigorous glossy, and it may be of use to give in detail the process as he now uses it.

The problem in a recent instance was to prepare a series of microphotographs at twenty diameters magnification of an embryo 26 mm. in length, cut transversely at  $20\mu$ , and stained with haematoxylin and eosin.

It was decided to photograph every tenth section. The Edinger projection apparatus was employed arranged horizontally, and a "Summar" lens of 115 mm. focal length. The distance from lens to paper holder (a frame fixed on a wall) was approximately 9 feet. The majority of the sections were of fairly uniform size, and the magnified image could be included in a sheet of paper 12 ins. by  $7\frac{1}{2}$  ins.

The other sections, which were of different size, could be taken on smaller sheets. The sheets purchased were 15 ins. by 12 ins., a size very generally useful as it can be cut without waste into a large number of different shapes to suit different sections. The work was done in a large room well lighted by

yellow light. The focussing of the image on the screen, to which the paper is afterwards fixed, requires to be done with great care and it is advisable to use a magnifying lens.

A coloured screen of pale green glass was interposed between the light and the section, and with the diaphragm fully open and with no substage condenser the exposure was about four seconds. A laboratory assistant was trained to assist in developing with a metol quinol developer—development takes only a minute or two—and with one assistant it was found that twenty to thirty photographs could be completed in the hour. The detail and the contrast in the prints was all that could be desired.

Of the value of such a series of microphotographs in working out the structure of an embryo and also for teaching purposes it is difficult to speak too highly. They are immensely superior to even the most careful drawings, and they can be prepared in a fraction of the time.

I have found it advisable to have a special album made up to hold the series of photographs of each embryo.

The method is one which I can thoroughly recommend for the purposes which it is intended to serve.

## A CASE OF RETRO-PERITONEAL HERNIA

BY JAMES FLEMING, M.B.

*Anatomy Department, Glasgow University.*

THE following condition was found in the abdominal cavity of a male subject dissected in the Anatomy Department of Glasgow University (October, 1922). The subject was an adult aged 70 years, and was well nourished, the cause of death being certified as cancer of the ear. On opening the abdomen, and turning up the great omentum, a large sac was observed occupying the area bounded above by the transverse colon, on the right by the ascending colon, and on the left by the descending colon. Below, the sac reached to the brim of the pelvis, and to the right side of the lower border a coil of small intestine was observed emerging from the interior of the sac. About four feet only of the small bowel lay outside the sac, and formed a loop which ended at the ileo-caecal junction. The loop was so disposed that the coil of bowel escaping from the sac emerged behind the terminal part of the ileum. In vertical and transverse diameters the sac measured 18 cms. by 17 cms. respectively. It appeared to lie more to the right side than to the left, and the hand could be passed behind the sac on the left side and so reach the middle line. Not so, however, on the right side, where the sac was limited by the peritoneum on the ascending colon, and above, where the transverse meso-colon seemed to limit its extension. Hence it was that the sac could be displaced bodily upwards and towards the right side, but not at all towards the left side. The caecum and appendix were normal, and there was a well marked ileo-caecal (bloodless) fold (pinned to the front of the sac in the sketch, fig. 6) and a very distinct ileo-caecal fossa. This fossa lay to the right and in front of the neck of the sac. The orifice of the sac lay behind the terminal part of the ileum and extended from the left or inner border of the caecum to the right side of the body of the fourth lumbar vertebra. By gently drawing on the bowel it was possible to deliver almost the whole of the small intestine from within the sac, but at the orifice the bowel was slightly adherent to the neck of the sac. Round the left margin of the neck there was very obvious torsion of the mesentery towards the cavity of the sac.

With regard to the margins of the sac, it was found that on the right side the covering of the tumour was continued laterally on to the ascending colon; above it became continuous with the under layer of the transverse meso-colon, but on the left side a marked difference was found. On displacing the sac bodily towards the right half of the abdominal cavity the attachment of the covering layer to the front of the vertebral bodies could be demonstrated, the layer there turning to the left as the posterior parietal peritoneum in that situation. Closer examination showed that while this description held good for the reflection on to the posterior wall at the base of the transverse meso-



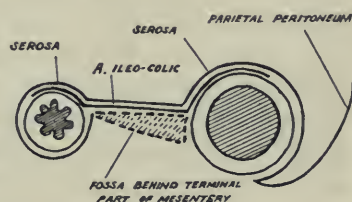
colon and at the level of the fourth lumbar vertebra, between these two points the finger could be passed for about an inch towards the right side between the sac and the peritoneum covering the front of the aorta. This, however, proved to be a pocket, from which the peritoneal covering of the sac passed again to the left as above and below. The mesentery could be felt in front of the finger at this point; consequently the pocket actually lay behind the root of the mesentery. Immediately in front of this part of the sac there was a prominent ridge-like fold running round the attached margin and appearing in front to cross the neck of the sac. When the sac was replaced in its proper position, the ridge only appeared at the neck of the sac (fig. 6) and was continued in the terminal portion of the mesentery to the caecum, in the attenuated ileo-colic fold. Here it became directly continuous with a similar ridge descending along the right limit of the sac. This second ridge turned to the left above, along the base of the transverse meso-colon. These ridges proved subsequently to be due to underlying blood vessels and appeared, by circumscribing it, to have determined the expansion of the sac.

Briefly, then, the sac appeared to be burrowing under the transverse meso-colon above, towards the ascending colon on the right, but to be limited on the left side by the tension in the peritoneal covering due to a large underlying blood vessel. In the interval between the caecum and the right side of the fourth lumbar vertebra, the loops of bowel escaped from the sac, behind the termination of ileum, and hung into the pelvis.

When the sac was opened the floor was found to be covered by peritoneum. This peritoneal layer was reflected off, near the left margin of the sac, to form a mesentery for that part of the bowel which could not be withdrawn from the sac. On the left side the extent of the floor of the sac corresponded with the limits of the sac as seen from without, but on the right side the peritoneal layer was seen to line a deep hollow to the outer side of the first part of the duodenum, and thence to be reflected on to the roof of the sac. It follows therefore that the wall of the sac as originally opened consisted of two layers, an outer layer as described above, and an inner lining layer continuous at the margins of the tumour with the peritoneum on the floor of the sac. Underneath the outer covering first described there was obviously a complete sac continuous in all directions, except at the neck. Here its floor passed to the general peritoneal covering of the iliac fossa, while its roof formed the posterior layer of the terminal part of the mesentery. The two layers forming the roof of the sac were therefore continuous round the terminal part of the ileum, and could be regarded as the modified mesentery of this segment of the small intestine.

The mesentery of that part of the bowel within the sac (i.e. that part which could not be withdrawn) was somewhat puckered, and not so well formed as is normally the case. Also it lay so very near the left (fixed) margin of the sac

FIG. 1.



that only a narrow sulcus here separated the bowel from the lateral wall. Between the two layers of the lateral wall at this point there lay the large vessel which caused the ridge referred to above.

The floor of the sac was next separated from the posterior abdominal wall and it was found that the duodenum was a straight tube, descending vertically with a slight inclination to the left from the pylorus, to be continuous with the small intestine, without any indication of a flexure. The duodenum lay completely behind the floor of the sac above, but as it descended it pushed its way into the sac so that about two inches from the lower border of the pancreas it appeared to have a mesentery. Lower down the mesentery appeared nearly normal. The pancreas was exposed by pulling down the inner (complete) sac, whose upper limit reached the root of the transverse meso-colon. This uncovered the origin of the superior mesenteric vessels, and here the artery gave off branches to be described later, and entered between the two layers of the so-called mesentery. The inner layer was thus proved to be a complete sac, the outer layer merely an anterior covering to it. The outer layer had obviously been the original peritoneum of the right half of the posterior abdominal wall, the inner layer an expansion of peritoneum pushed before the herniating bowel.

*Blood vessels.* On the left posterior abdominal wall the inferior mesenteric vein and the left colic branch of the corresponding artery (the vascular arch of Treitz) were in their normal position, and had absolutely no relationship to the sac. Naturally there were no duodenal fossae, as the duodeno-jejunal flexure had been pulled out into a straight tube. The superior mesenteric artery appeared at the lower border of the pancreas and immediately gave off from its anterior aspect a large trunk which proceeded under the transverse meso-colon, and then divided into branches for the colon (mid-colic) and a large branch which proceeded laterally along the root of the meso-colon towards the hepatic flexure. Here this branch turned downwards and reached the caecum (fig. 2*a*). This was the right colic artery, which normally passes directly to the ascending colon from the concavity of the parent trunk (fig. 2). This vessel was responsible for the ridge-like fold already described in the upper and right margins of the sac. At the ileo-caecal junction it was directly continuous with the blood vessel in the other ridge mentioned. This latter proved to be due to a large vessel which sprang from the left side of the superior mesenteric artery about half an inch below the combined origins of the right and mid-colic arteries. It was taken to be the ileo-colic artery which normally springs from the right side of the superior mesenteric and proceeds to the ileo-colic angle. The junction of these two vessels was tightly stretched across the neck of the sac, and here the appendicular artery was given off by the ileo-colic, this branch being an anterior relation to the right margin of the neck of the sac. These two vessels were apparently displaced by the enlarging sac, the ileo-colic to the left and below, the right colic to the right and above. From their relative positions it was therefore concluded that the sac had primarily pushed its way forward between these two vessels at a point marked

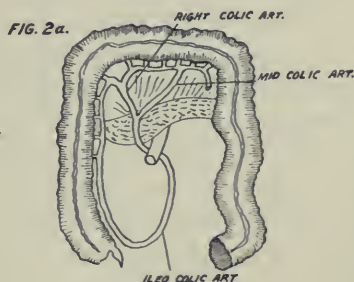
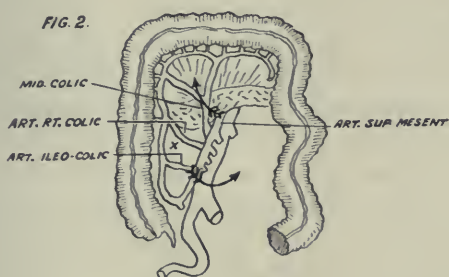


(X) in fig. 2, pushing the one downwards as it expanded, and the other upwards. Stretching of these vessels would tend eventually to limit this expansion.

Nothing else abnormal was found in the abdomen except (1) that the common and external iliac arteries took a sharp bend downwards into the true pelvis and then ascended straight to the femoral sheath, and (2) that the left renal vein joined the vena cava as two trunks separated by about two inches, the one passing in front of, and the other behind the aorta.

In considering the mechanics of this remarkable hernia, Moynihan's(1) essay on retro-peritoneal hernia has been freely consulted as an epitome of the literature up to that time (1906). Rendle Short(2) in the *British Journal of Surgery*, vol. III, brings the literature further up to date (1916). Moynihan describes various folds and fossae and gives a classification of retro-peritoneal herniae. Of these it will only be necessary to refer to three main varieties, viz. left and right duodenal hernia, and hernia occurring in the region of the caecum.

With regard to left duodenal hernia, Moynihan emphasises the facts (1) the inferior mesenteric vein must be in the neck of the sac, (2) the sac must



burrow upwards or to the left towards the descending colon. The present specimen obviously cannot come into this category. Right duodenal hernia would seem to be a much more plausible diagnosis, and one has been at some pains to exclude this. To quote Moynihan again: (1) The sac occupies, at any rate at first, the right half of the abdominal cavity, lying behind the ascending and transverse meso-colon. (2) The orifice is situated behind and to the left of the sac, on the lumbar vertebrae. (3) In the anterior margin of the sac there lies either the superior mesenteric artery or its direct continuation the ilco-colic artery.

In this case, however, the orifice of the sac was below and to the right, the superior mesenteric artery was, strictly speaking, behind the sac, and only the position of the ilco-colic artery in the neck of the sac could in any way correspond with the description of a right duodenal hernia. Such a hernia involves the fossa of Waldeyer (Moynihan, *loc. cit.*), which lies within the concavity of the arch formed by the superior mesenteric artery. Its orifice looks to the left, its fundus to the right and downwards, while behind it are the lumbar vertebrae covered by peritoneum. As a hernia in such a fossa increases, it



strips the peritoneum up till the duodenum is reached, this portion of the gut eventually forming a posterior relation to the neck of the sac. The orifice may increase downwards and to the right until the ileo-caecal junction is reached, as in Gerard-Marchant's(3) case. In the present case, however, the neck lies to the right at the ileo-caecal junction and moreover the duodenum is pulled out straight and obviously has no relation to the neck of the sac. From Moynihan's description, therefore, a right duodenal hernia may justifiably be excluded.

Turning now to the ileo-colic area, the possibility of certain fossae having to do with the hernia must be considered.

(1) The superior ileo-caecal fossa (Treves(4)) was obliterated by the stretching of the ileo-colic fold with the included ileo-colic artery tightly across the neck of the sac.

(2) The inferior ileo-caecal fossa was distinctly in front of the neck as seen in the sketch (the bloodless fold is pinned to the front of the sac).

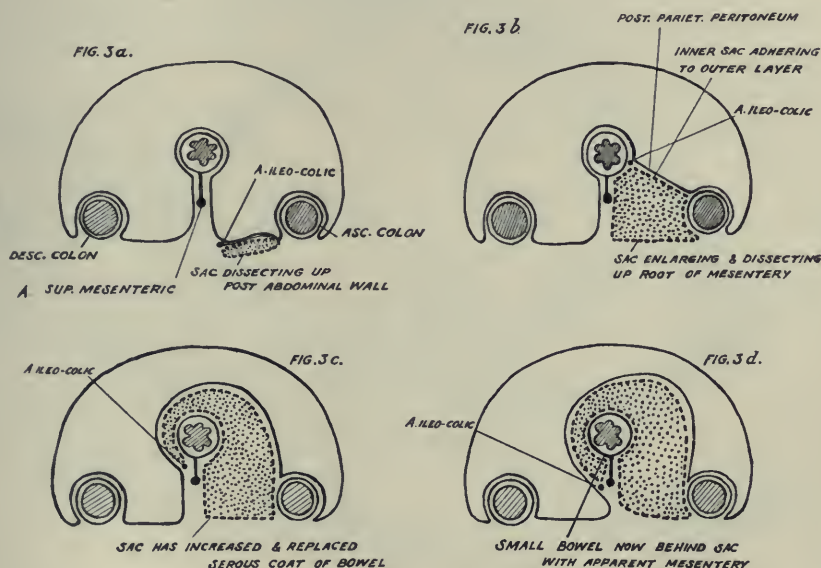
(3) There were no fossae behind the caecum or the ascending colon, consequently retro-caecal and retro-colic herniae can be excluded.

At this stage it may be well to attempt to elucidate the meaning of the curious arrangement of peritoneal layers found in connection with this tumour, turning later to the merely speculative discussion as to its origin. If it be granted that the bowel entered some fossa, normal or abnormal, lying behind the terminal part of the mesentery, and immediately to the left of the caecum, a ready explanation can be found.

Fig. 1 shows the last part of the mesentery and the caecum in section. The ileo-colic artery anastomoses with the termination of the superior mesenteric between the two layers of this part of the mesentery. Given a fossa here, it would have two layers in its roof with the artery between them, and as its floor the peritoneal lining of the iliac fossa. Bowel entering the fossa would lie behind the terminal part of the ileum and if it increased it would always have the same relations to its floor and roof as it had at the neck. That is, it would have the anterior and posterior layers of the mesentery in front of it, and the lining of the iliac fossa behind it. But the anterior layer of the mesentery, traced up, is continuous with the under layer of the transverse mesocolon; traced laterally to the right it covers the ascending colon, while to the left it covers the small bowel and then the posterior abdominal wall on the left of the root of the mesentery. This corresponds to the outer layer of the sac as described, and if the forward bulging of the sac occurred primarily at the position (X) in fig. 2, the limits would be determined by the constricting action of the stretched right colic and ileo-colic arteries, and the latter artery swinging to the left with the growing sac, would appear to arise from the left side of the parent trunk. The case of the right colic artery is not quite so clear, arising as it does in common with the mid-colic, but that it has been displaced upwards cannot be doubted.

The herniating loops may thus be imagined to have pushed in front of them a sac which dissected up the posterior parietal peritoneum, and as it did so,

replaced that layer with its own floor, while its roof adhered to the layer it was stripping up. This means that from the level of the ileo-caecal junction below to the transverse meso-colon above, and laterally to the ascending colon, the peritoneum was, as it were, blown off the abdominal wall from behind, but as this was taking place the sac proper invested the structures, thus denuded, with its own peritoneum. As the process extended medially the ascending loop of the duodenum was stripped along with the attached suspensory ligament of Treitz. This brought about a ptosis of the duodeno-jejunal flexure. Meanwhile the peritoneum was stripped up from the root of the mesentery, off the bowel itself, and so on until the left side of the root of the mesentery was reached. Then the bowel continuous with the descending part of the duodenum was stripped and pulled out straight, the floor of the sac was spread over it, and by thrusting itself forward the denuded gut contrived to acquire a new

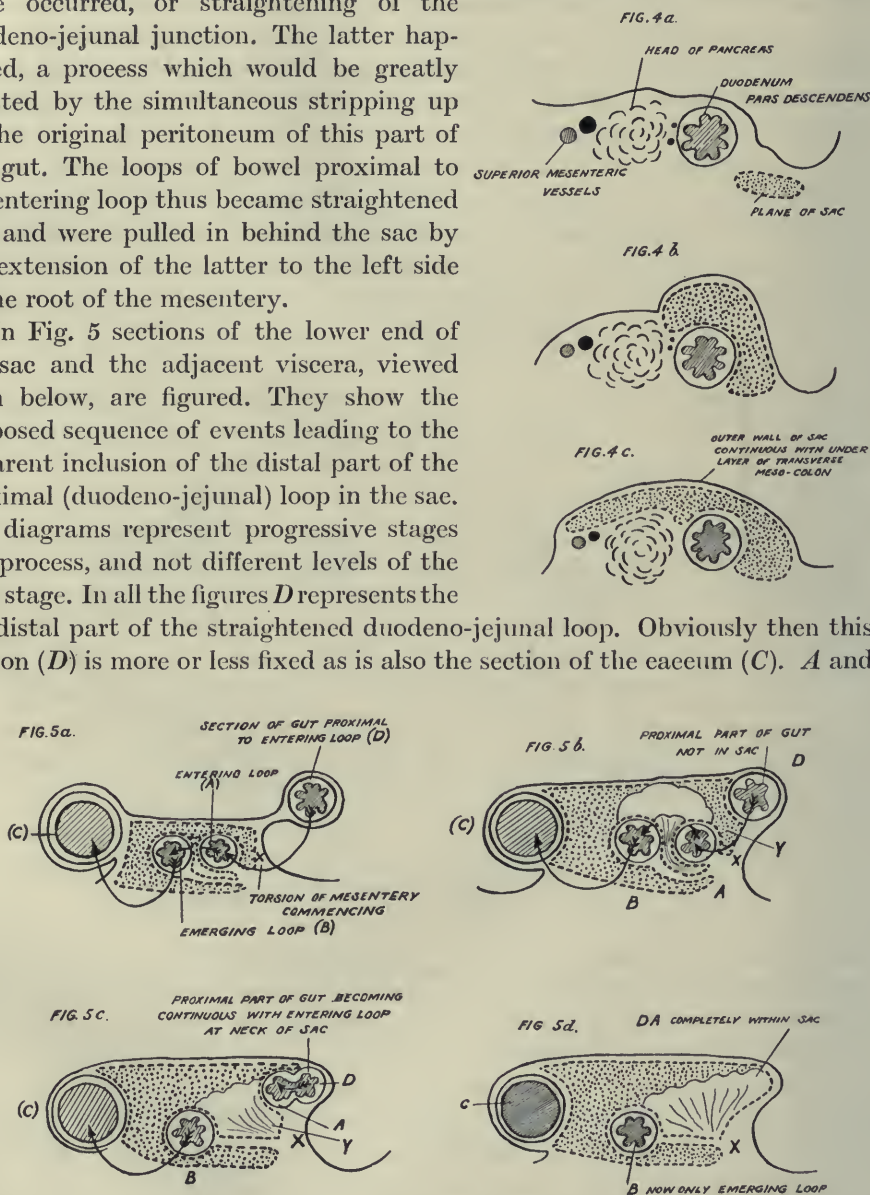


mesentery from the floor of the sac. A reference to figs. 3 and 4 (sections viewed from above) will explain in detail how this metamorphosis may have been brought about, and how the superior mesenteric artery has maintained its original relationship to the bowel.

Further, the spread of the inner sac to the left lateral side of the root of the mesentery would tend to be limited by the stretching of the ileo-colic artery which, originally lying beneath the peritoneum of the right posterior abdominal wall, has now been swung to the left, and lies between the outer and inner layers of the sac at its left attached margin. All this has been brought about by the sucking into the cavity of the sac of more and more loops of small intestine. The primary entering loop presumably lay below the ileo-caecal junction originally. Such an entering loop would draw in bowel both proximal and distal to it, but from the general direction of the peristaltic

waves it would be more likely to use up the bowel which lay proximal. Assuming then that it did so, a time must have come when the proximal part of the bowel was pulled taut. Then either strangulation of a loop must have occurred, or straightening of the duodeno-jejunal junction. The latter happened, a process which would be greatly assisted by the simultaneous stripping up of the original peritoneum of this part of the gut. The loops of bowel proximal to the entering loop thus became straightened out, and were pulled in behind the sac by the extension of the latter to the left side of the root of the mesentery.

In Fig. 5 sections of the lower end of the sac and the adjacent viscera, viewed from below, are figured. They show the supposed sequence of events leading to the apparent inclusion of the distal part of the proximal (duodeno-jejunal) loop in the sac. The diagrams represent progressive stages of a process, and not different levels of the final stage. In all the figures *D* represents the cut distal part of the straightened duodeno-jejunal loop. Obviously then this section (*D*) is more or less fixed as is also the section of the caecum (*C*). *A* and



*B* represent sections through the entering and emerging loops respectively of the herniating small bowel. It will be equally obvious that the particular part of the bowel thus represented will not be constant. In other words the section is meant to indicate the parts of the small bowel which at different



stages lie in the neck of the sac. Naturally as the hernia enlarges an ever increasing length of bowel will separate *A* from *B*. The cavity of the sac is stippled, and represents a section immediately above its neck. The arrows indicate the proximal and distal connections of the two limbs of the herniating gut, the region marked (*X*) the position of the supposed torsion and stretching of the mesentery. For the sake of simplicity the mesenteric attachments of the herniating loops are represented as double, i.e. a double peritoneal layer is figured as passing to each sectioned lumen.

FIG. 6.



This general statement describes the state of affairs in fig. 5 *a*. In fig. 5 *b* it will be noticed that the arrow indicating the coil of bowel joining *D* to *A*, is being pulled more into the sac, and this loop is gradually being undone. More bowel is now in the sac, and the continuity of the entering and emerging loops is indicated by lines joining them. The continuity of their mesenteries is also suggested by the thin black lines. It will be clear from this diagram that the lining of the sac at the point (*Y*) has only to be thrown over the wall of the gut intervening between *D* and *A*, in order to get the appearance shown in the next figure. This of course can only have been brought about by the stripping of the serous coat of *A* by the expanding lining of the sac. In fig. 5 *c*, *A* and *D* are almost continuous, and the peritoneum at (*Y*) has become the mesentery joining *DA* with *B*. In the next figure (5 *d*) the process is completed and the mesentery of *A* is one with the mesentery of *D*, the loop thus formed

projecting upwards into the cavity of the sac, immediately above its neck. In the last section, actually through the neck of the sac, only the emerging loop appears.

A large hernia developing in such a way must of necessity have grown very slowly and presumably have started in very early life. As the caecum and appendix were normal in position and there was no ascending meso-colon, evidently the rotation of the gut had occurred in its usual way and the downward growth of the caecum had been completed. A fossa of Hartmann is described (recessus post-iliaci of Tarentzky (5)) as lying behind the meso-appendix. "In some cases the lower attachment of the mesentery to the iliac fossa is prolonged into a sharp fold...it springs from the ilco-colic angle and from the posterior and inner aspect of the caecum, and runs backwards to the iliac fossa." (Moynihan, *loc cit.*). It is generally accepted that a case described by Snow (6) occurred into this fossa. A fossa in this position might conceivably determine the formation of the hernia, with the termination of ileum, the meso-appendix and its artery, lying in front of its orifice.

To summarise the points about this hernia:

(1) A sac growing chiefly at the expense of the peritoneum to the right of the root of the mesentery.

(2) An anterior covering to the sac formed by the pushing forward of the right half of the posterior parietal peritoneum.

(3) The sac overlapping the straightened duodenum.

(4) This straight tube lying behind the sac but by its forward projection into the sac, appearing to have a mesentery. (This tube was about one foot in length.)

(5) This apparent mesentery becoming continuous, at the neck of the sac, with the true mesentery of the most proximal loop of herniating bowel.

(6) The true mesentery greatly twisted and elongated at the left margin of the neck of the sac in order to permit the greater part of the small bowel entering the sac.

(7) A single emerging loop, slightly adherent to the neck of the sac, and distant about four feet from the ileo-caecal junction.

(8) Termination of ileum in front of the neck of the sac.

(9) Neck of the sac bounded in front by (8), to the right by the caecum, to the left by the root of the mesentery, and behind by the peritoneum of the iliac fossa.

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## A LARGE DIVERTICULUM OF THE URINARY BLADDER

By CECIL P. G. WAKELEY, F.R.C.S. (ENG.).

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CONGENITAL diverticula of the bladder may be classed into two principal groups:

(1) Those arising in relation to the allantoic tube, and consisting of an urachal cyst opening near the summit of the bladder, and connected by the urachus with the umbilicus.

(2) Those involving the lower end of the ureter, or opening into the bladder in the vicinity of an ureteral orifice; to which category the present specimen belongs.

Urachal or allantoic cysts are well known and have been described by Lawson Tait (*Brit. Gyn. Journ.* vol. II. p. 328), and other authors. They are lined by a stratified layer of epithelium corresponding to that of the normal bladder and the walls consist of fibrous connective tissue containing unstriped muscle.

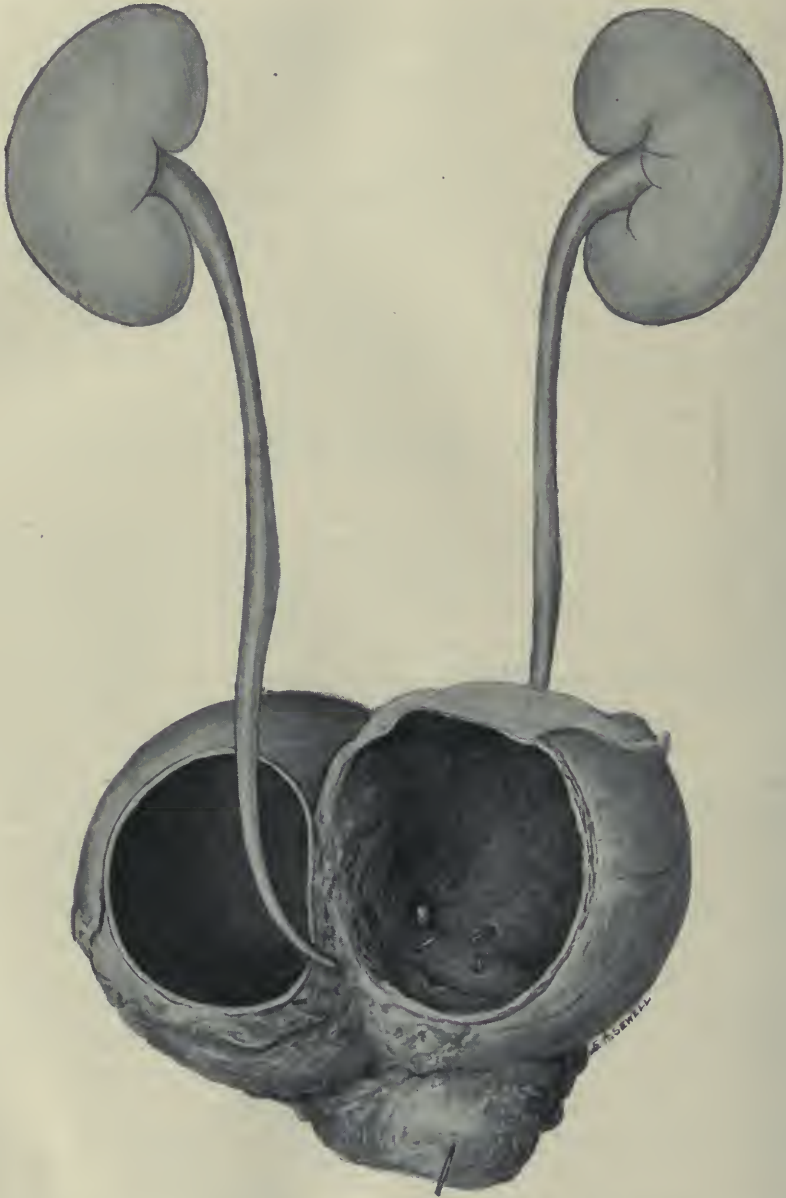
The second group of cysts or diverticula connected with the bladder have been described under the titles, supernumerary bladders, multiple bladders, duplication of the bladder, etc. Some of these cases probably represent an exaggeration of the acquired condition of sacculation and are generally accompanied by stricture of the urethra or some obstruction to the outflow of urine. Other cases are unaccompanied by any sign of obstruction and may consist of two symmetrically placed sacs, right and left, opening into an otherwise normal bladder near the ureteral orifices and have all the appearances of a congenital abnormality.

A case was described by Erichsen (*Science and Art of Surgery*, p. 1129) in which two enormous sacs opened into the bladder, one on each side about  $1\frac{1}{2}$  inches above the opening of each ureter and equidistant from the median plane. The openings of the diverticula were rounded and sufficiently large to admit the tip of the little finger. The walls were thin and composed chiefly of mucous membrane and peritoneum, possibly a few scattered muscle fibres; the ureters were adherent to the cyst wall and compressed. The pelves of the ureters were dilated and the pyramidal portion of the kidneys absorbed.

In one case reported in Treves' *System of Surgery* a woman was found to have five bladders, five kidneys and six ureters. Such cases indicate the possibility of these abnormalities being due to the formation of accessory renal diverticula which may or may not become connected with the metanephros.



In some specimens the bladder is divided by a median septum. A possible explanation of this condition is the enlargement and persistence of the "cloacal



horns" of the ventral part of the cloaca which forms such a prominent feature of the developing bladder at the 11 mm. stage before the lower end of the mesonephric duct has become included in the cavity of the bladder to form the trigonum vesicae.

The patient from which this specimen was removed was a male *aet.* 50 years

who died from uraemia three days after admission to hospital. Just prior to admission the patient consulted his doctor because he felt ill and drowsy and was suffering from diarrhoea. He was a big man and on examination he was found to have some diminished resonance at the left base and some very fine crepitations; he was coughing but could not bring up anything, the heart was normal, the pulse was about 100, and the respirations were 28. There was no tenderness in the abdomen. The urine on examination was found to contain blood casts and *B. coli* in large numbers. There seemed sufficient in the left base to make this a case of pneumonia and to dispel the supposition of surgical kidney. There had been no pain in the loins and there was no tenderness over the kidneys, and the blood pressure was not high. The patient was kept in bed and the signs in the lung cleared up after a few days. However, a few days later the patient developed coma and was admitted to hospital; he died after two days without regaining consciousness. He was catheterised and no stricture was present. There was no history of syphilis or gonorrhoea. Post-mortem examination revealed a very large diverticulum of the bladder, it seemed about the size of half a distended bladder and its capacity was about 10 ounces. It was situated on the right side of the bladder and communicated with that viscus by a round hole which would just admit a pencil. The edges of the orifice were sharply defined. The bladder wall was a little thickened owing to the chronic cystitis which was present. There were no signs of any other diverticula or pouches in the bladder, nor was there any sacculation or trabeculation. The orifice of the diverticulum was situated just above the right ureteral opening. Both ureters were thickened. The kidneys were not enlarged and on microscopical examination the vessels of the kidney substance, especially those accompanying the renal tubules, were found to be engorged. Except for some pneumonic patches in the left lung the rest of the body appeared normal. A section of the wall of the diverticulum revealed the presence of muscle fibres; this fact some investigators including Virchow and Englisch consider of importance because they state that when muscle is present in the diverticulum it is congenital and when absent it is acquired. In the Johns Hopkins' *Hospital Reports* for 1906 Young always found muscle in the walls of the diverticula he examined although in some cases the layer was very thin.

It is a question if diverticula of the bladder are ever acquired. Sir John Thomson Walker in his well known text-book on *Surgical Diseases and Injuries of the Genito-urinary Organs* states: "While many of the diverticula are congenital, some are apparently due to urethral obstruction, and are met with in cases of stricture and enlarged prostate. In some cases I have found a history of pelvic cellulitis (from appendicitis salpingitis, etc.) and traction from without by adhesions may have been a factor."

Hyman (*Surg. Gynec. and Obst.* Jan. 1923) reports three interesting cases of diverticula of the bladder in children, and he is of the opinion that undoubtedly there will be an increase in the number of cases reported as soon as cystoscopy in children becomes more of a routine procedure.

## ANOMALOUS CARPAL BONES

By E. JOYCE PARTRIDGE, F.R.C.S.

*The London School of Medicine for Women.*

THE accompanying sketches are illustrations figs. 1 and 2 of a right carpus and fig. 3 of the left unciform found in the same dissecting room subject. It will be seen that the trapezoid in the articulated carpus is apparently divided into two halves as is also the disarticulated unciform from the opposite hand.

Fracture as a cause of the condition can be eliminated as the trapezoid exhibited a perfectly symmetrical arrangement in the two hands, and in these circumstances the unciform may also be regarded as sharing in the same anomalous development.

These divisions of bone, granted that they are not fractures, are to my mind worth recording because of their probable embryological significance.

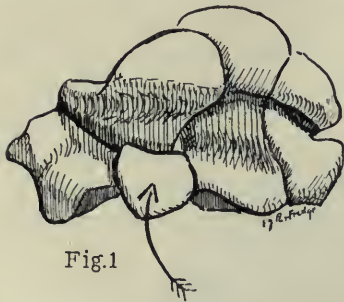


Fig.1

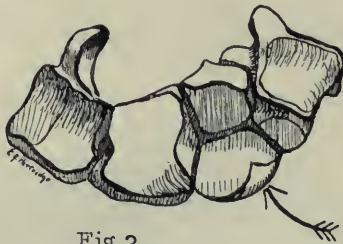


Fig.2



Fig.3

That the unciform represents the fusion of two elements (carpalia of the primitive type of fore limb) of the distal row is a generally accepted view. Although the hamulus is known to chondrify independently I cannot find a description of the extension of this independent chondrification into the body of the bone as is shown in the illustration (fig. 3). Do the two ossicles represent elements which are independent in the primitive carpus, and if such be the case why are they disposed in an antero-posterior plane and not placed side by side, are questions of some considerable interest.

With regard to the trapezoid as shown in figs. 1 and 2, the question arises as to whether its division is simply a peculiarity of development of this bone, or whether either part of this bone represents an element usually lacking from the human hand, but found in more primitive types.

Leboucq expressed the view that in the human carpus the centre of chondrification corresponding with the os centrale fuses in all probability with the scaphoid, and enters into the formation of its posterior border just below the



oblique ligamentous ridge. When an os centrale appears as a separate bone, it is said to be found always on the posterior surface of the carpus in the angular interval between the scaphoid, the os magnum and the trapezoid. Admitting it to be possible for the os centrale to appear in these two different ways, is it not conceivable or even easy to imagine that it may undergo a still further distal displacement, appear on the back of the trapezoid, and assume the form shown in the illustration of the carpus?

In this connection it is interesting to note, that the carpal bone most commonly found divided by Pfitzner was the trapezoid; indeed he described a new supernumerary carpal bone in the form of the "Trapezoide Secundarium." Perhaps his description of this division of bone was only an indication of the frequency with which the os centrale appears at the back of the trapezoid.

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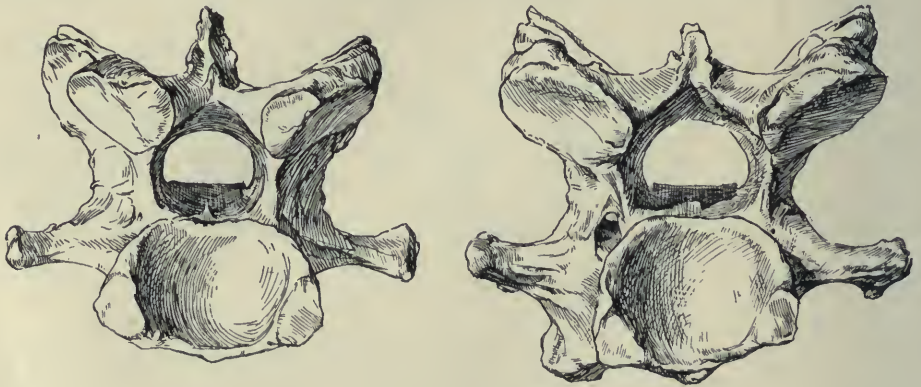
## ABNORMAL CERVICAL VERTEBRA OF HORSE

By B. GORTON, M.R.C.V.S.

DURING the examination of the carcase of a horse which was destroyed recently, it was noticed that the seventh cervical vertebra was abnormal.

Normally the lateral process of this bone is a single outwardly projecting process which does not present at its root a foramen transversarium found in a typical cervical vertebra. The inferior or ventral spine, on the ventral aspect of the centrum, is an elongated bifid ridge quite small in size. The dorsal spine (spinous process), on the other hand, is conspicuous and is a definitely outstanding prominence.

In the abnormal vertebra under consideration the lateral process on the right side is normal, being single and untraversed by a foramen; on the left



side, however, the process is double, having two well marked prominences, a dorsal projecting outwards and a ventral projecting downwards. The dorsal part, which has a blunt extremity, is apparently the counterpart of the whole process on the right side. It is significant that the ventral prominence is in line with the capitular facet for the first rib which, in the horse articulates with the seventh cervical vertebra as well as with the first thoracic. The root of the process is pierced by a large foramen.

The inferior spine, on the ventral aspect of the centrum, is represented by a rounded ridge not quite median in position.

Another departure from the normal is seen in the fact that the right capitular facet for the first rib is slightly more dorsal in position than that on the left.

The asymmetrical condition scarcely calls for comment, as anomaly involving a vertebra is most frequently one sided.

The condition on the left side may be explained by regarding the dorsal prominence of the lateral process as representing the transverse process proper, and the ventral process as being costal in nature. In the normal seventh cervical vertebra the transverse and costal processes are indiscriminately fused, as is the condition on the right side. On the left side, however, the distinction between the two is accentuated not only by the presence of a costo-transverse foramen, but by the distal independence of the greater part of the costal element.

In short there is apparently an asymmetrical attempt at the exhibition of a cervical rib.



## ON MAXIMUM ARM STRETCHING

BY EDGAR F. CYRIAX, M.D. (EDIN.).

*London.*

LET it be supposed that a subject assumes what is known in Swedish drill nomenclature as "yard" position, i.e. he abducts both arms until they come to lie horizontally outwards, keeping his scapulae drawn backwards and inwards the whole time<sup>1</sup>. From this position it is possible by active effort to perform "maximum arm stretching sideways," i.e. to stretch the arms still further horizontally outwards thereby increasing their lateral span by two inches or more. This movement is one which with various modifications as regards direction, such as being combined with different amounts of flexion and abduction and the reverse, is continually being used in many games and sports in which efforts of greatest stretch in order to reach a ball or a person, play such an important part.

The mechanism involved in this arm stretching cannot be found described in any books on physical drill or athletics, and almost all anatomy books entirely ignore it<sup>2</sup>. Not only this but enquiries from both medical men and physical training experts have shown me that there is a wide-spread and erroneous belief that such maximum arm stretching sideways is effected by contraction of the muscles of the arm and forearm. This mistake has probably arisen because such muscle contraction is involuntary and nearly always accompanies the stretching, but it is of course obvious that it cannot actually cause any elongation, as it is impossible that contraction of muscles passing over a joint can do otherwise than approximate its opposing articular surfaces. Further, it can easily be shown that such arm and forearm contraction does not assist at all in the stretching because it can be performed equally well (if indeed not a little better) while the arm is kept resting on a horizontal table with all its muscles relaxed.

In order to discover the mechanism involved I examined a number of subjects of all ages and both sexes; some of these were quite used to physical drill and games, others were quite the opposite. This factor, however, does not cause any material differences in what takes place during the arm stretching, the component parts of which are as follows:

1. *Scapula*. This bone moves around the chest wall en masse, rotating as it goes so that the acromion becomes elevated to a greater degree than the

<sup>1</sup> Compare the author in *Journ. Anat.* LI. 396-399. 1916-17.

<sup>2</sup> The only exception that I know of is Quain (*Elements of Anatomy*, II. pt. 2, 213, 1892) who makes the brief statement that "the serratus magnus, by withdrawing the base of the scapula from the spinal column, enables the arm when raised from the shoulder to be still further out-stretched, as in the movement termed extension in fencing."

upper angle. There is a tendency to elevate the scapula as a whole, but this leaves the greatest span obtainable practically unchanged.

2. *Clavicle*. During the first part of the movement this bone follows the movements of the scapula, i.e. its acromial end moves forwards and upwards, a rotation occurring round a centre in the sterno-clavicular joint. This may be all that takes place, continuing in this way until the maximum stretching has been performed, but in many persons, chiefly young subjects and in those used to physical drill, as the stretching proceeds, the interval between the sternal end of the clavicle and the sternum widens, and the whole bone moves a little outwards en masse; in addition the sternal end of the bone may move backwards, finally attaining a position as much as  $\frac{1}{4}$  inch or even more behind its original site. This last mentioned movement backwards of the head of the bone diminishes in direct proportion to the amount that the arm is carried backwards during the stretching movement, and the reverse occurs when the arm is carried forwards.

Most anatomy books refer to the possibility of gliding movements taking place between the clavicle and acromion. During maximum arm stretching sideways such lateral gliding would, if it existed, be of great service in increasing the lateral span, but none can be detected either by inspection or palpation, and I am indebted to Dr R. L. Rawlinson for having screened several cases for me and with the X-rays proved that no such gliding movement took place.

The movements of the clavicle just described are as far as I can judge merely a passive accompaniment of the movements of the scapula and are not brought about by any active contraction of its integral muscles.

3. *Humerus*. It is evident that were the gleno-humeral joint kept immovable during the maximum arm stretching sideways, the whole upper extremity would be moved en masse forwards and upwards as the scapula advanced. In order to prevent this and keep the arm continually horizontal, the humerus must, as the scapula moves, be relatively abducted and moved backwards in the horizontal plane.

Concerning the muscular actions involved in the arm stretching, apart from the involuntary contraction of most of the muscles of the extremity, as already mentioned, which has no effect whatever upon the stretching *per se*, there is also a simultaneous contraction of many of the muscles of the shoulder girdle in order to keep the arm abducted and to give that necessary fixation without which no movement can proceed. This at first makes it very difficult to distinguish between such muscles of fixation and muscles actually performing the stretching. If, however, the arm be first abducted to a right angle and the elbow semi-flexed and the whole arm supported by resting it on a table, the fixators are thrown out of action and only those muscles will contract which are actually concerned in the movement.

With the arm in this position definite signs of contraction were found in two muscles only, the serratus magnus, which moved the scapula round the chest wall, and the posterior third of the deltoid, which moved the humerus

backwards. The lower fibres of the serratus magnus appeared to act more powerfully than the upper, but this point could not be determined easily owing to the thickness of the subcutaneous fat and to the condition of tension of the two axillary folds.

During the last stage of the stretching the subject frequently experiences tingling sensations in the arm as a whole, specially its anterior aspect. The sensations in the forearm are generally relieved by relaxing the forearm muscles and flexing the wrist, and the sensations in the entire arm are similarly affected by flexing the elbow joint, even if the surrounding muscles are not relaxed. It is therefore highly probable that the sensations in question are due to elongation of the nerves of the front of the arm and not to any pressure upon them in the axilla or on the blood vessels in this region.

In conclusion I may state that I examined two pathological cases, namely one of "floating clavicle"<sup>1</sup> and one of cleidocranial dysostosis in which one clavicle was entirely absent and the other represented by a cartilaginous rudiment about three inches in length, and found that as far as the scapula and humerus was concerned their behaviour during maximum arm stretching sideways appeared to be identical with that of normal subjects.

<sup>1</sup> See the author, *Anat. Rec.* xvi. 379-380. 1919.



# ON "EXCENTRIC" CONTRACTION OF MUSCLES

BY EDGAR F. CYRIAX, M.D. (EDIN.).

*London.*

FOR the performance of voluntary movements there are two distinct kinds of muscle contraction, namely:

(a) Where the contraction of the muscles is able to overcome the resistance offered to them, and they thus become shortened,

(b) Where the resistance overcomes the contraction of the muscles, which thus become elongated.

The first person who scientifically distinguished between these two varieties of muscle contraction and who employed them from the therapeutic aspect was the Swede P. H. Ling (1776–1839), in whose system the so-called resisted or "duplicate" movements played such an important part. These exercises, according to where the resistance was applied, brought into play either the same muscles continuously or else antagonistic ones alternately. The terms used by Ling and his school to express the two kinds of contraction mentioned were either "half-active" or "active-passive" when the muscles shortened, and "half-passive" or "passive-active" when they elongated; these terms were, however, somewhat misleading as there was no passivity in any of them. About 1847 Neumann<sup>1</sup> introduced the terms "concentric" and "excentric" respectively which have superseded the former ones and have been retained ever since in Swedish gymnastic literature. For this reason I have adopted them in this paper.

Now although writers on anatomy, clinical medicine and neurology do full justice to concentric contraction of muscles they almost totally ignore the fact that there is such a thing as excentric contraction thereof. This is all the more surprising because physiology text-books give it a good deal of their attention. As regards the first mentioned authors, the only hint of the existence of excentric contraction is found in a few anatomy books who mention that adduction of the previously abducted humerus is performed by the adductors assisted by the weight of the arm (see A below) and that the weight of the lower jaw plays a part in depression of the same. Otherwise the possibility of gravity playing a part in any other movement is never entertained.

Neglect to take into account the existence of excentric contraction of muscles is in my opinion largely responsible for a number of statements in the above text-books which are either incomplete, or at best only partially

<sup>1</sup> *Wochenschr. f. d. ges. Heilk.*, 1849, pp. 229, etc., 1850, pp. 65, etc.; *Die Heilgymnastik*, 1852, pp. 15, etc.

correct, and which have in consequence led to many misconceptions. The following examples will show this:

*A. Adduction of the shoulder joint.*

One frequently meets with statements to the following effect: "Abduction is performed by the deltoid and supraspinatus, assisted by certain other muscles that rotate the scapula....Adduction is performed by the adductor (pectoralis major, teres major, subscapularis, latissimus dorsi) aided by the weight of the arm...." It is a curious fact that one never finds any mention of the fact that the scapula during such adduction goes through the reverse of what it did during abduction, some of its muscles contracting concentrically if resistance is being offered to the movement. Furthermore the latter half of the statement is correct only in the following instances:

(a) When resistance is opposed to the movement which the unaided weight of the arm is either totally unable to overcome or else cannot do so with sufficient rapidity.

(b) When the movement has to be performed with great speed as for example in the case of defensively bringing the arm sharply to one's side after receiving a sudden dig in the ribs.

In all other cases, the muscular mechanism is one of the following:

(a) When the subject who has abducted his arm, suddenly relaxes the abductors, thereby letting the arm drop passively to his side; then the movement is effected by the weight of the arm alone, the adductors not undergoing any concentric contraction, but merely becoming passively shortened.

(b) When the subject who has abducted his arm performs co-ordinated adduction in the absence of any opposing force. The movement is then brought about by excentric contraction of the abductors, thus allowing the weight of the arm to overcome them. Just as in (a) above, the adductors merely undergo passive shortening.

*B. Lateral flexion of the trunk on itself.*

One frequently encounters statements to the following effect: "The two halves of the erector spinae (and its prolongations) acting simultaneously maintain the erect position and extend the trunk....Flexion of the trunk to one side is produced by the contraction of the erector spinae of that side...." The latter half of this statement is correct only in the following instances:

(a) When the movement has to be performed with great rapidity, as is the case in many games in order to reach a ball, etc. Even under these circumstances the lateral flexors of that side to which the bending is performed relax towards the end of the movement, the corresponding muscles on the other side undergoing progressively increasing excentric contraction, this being done in order to modify the speed of the movement and to prevent overstrain and possibly sprains arising in the back.

(b) When the subject to commence with is in such a position that the pull of gravity is either eliminated, as when lying on his face or back, or else re-

versed as when lying on the side opposite to the one which is to be laterally flexed (and of course in all intermediate positions between the two).

(c) When resistance is offered to the side of the body that is to become laterally flexed, provided that it be in sufficient amount to prevent gravity performing the movement unaided, i.e. without the help of the lateral flexors of that side.

In all other cases the muscular mechanism involved may be divided into three stages which are not of course absolutely distinct, but slightly overlap. For the sake of convenience of description it will be assumed that the flexion is to take place to the left side, and the following is the sequence of events:

(a) The lateral flexors of the right side transform their static into excentric contraction, those on the left side changing theirs into passivity. Gravity will thus be enabled to produce the flexion to the left, the right lateral flexors becoming elongated and the left ones shortened.

(b) As the movement proceeds, the gradually increasing elongation and tension in the right lateral flexors offers progressively increasing resistance to the flexion, thus proportionately relieving these muscles of the necessity for excentric contraction, until finally a point is reached when the amount of the latter becomes nil.

(c) The left lateral flexors then commence to undergo concentric contraction and they continue to do so in continually increasing amount until they together with the pull of gravity to assist them cannot bring about any further elongation of the right lateral flexors. The physiological limit of the movement has then been reached.

The reverse stage of the movement is of course effected by concentric contraction of the right lateral flexors overcoming the pull of gravity on the left side and passively elongating the left lateral flexors.

The fact that the theory is so prevalent that lateral flexion of the side is caused by concentric contraction of the muscles of the same side is, I consider, largely responsible for the widespread erroneous view that in cases of lateral curvature the muscles on the concave side are contracting more powerfully than their antagonists. If this were true, it would be impossible to assume the erect position at all as a rapid and powerful trunk flexion to the concave side would result as soon as this was attempted. It is of course evident in such curvatures that the muscles on the convex side must in order to maintain the erect posture contract as much as those on the concave side plus the unopposed force of gravity acting down that side.

### *C. Flexion forwards of the trunk on itself.*

It is generally stated that this movement is brought about by contraction of the various anterior muscles of the trunk. But, just as in the case of lateral flexion of the trunk on itself, so is this statement true only in the case of having to execute the movement very quickly, or where the pull of gravity is eliminated as when lying on the side, or reversed as when lying on one's back (and in intermediate positions), or when resistance is applied to the front of



the body. In all other cases this movement is performed by excentric contraction of the erector spinae which diminishes until it becomes nil, at which juncture the force of gravity which cannot elongate these muscles any further is reinforced by progressively increasing concentric contraction of the anterior muscles until the physiological limit is reached. The reverse movement is of course effected by concentric contraction of the erector spinae<sup>1</sup>.

*D. Testing the power of muscles by noting the results of efforts to perform certain movements.*

One frequently finds statements to this effect: "Inability to flex the foot points to paralysis of the anterior tibial muscles, such as is frequently the case in infantile paralysis...." "Inability to extend the wrist and fingers is indicative of paralysis of the extensors on the back of the forearm, as is seen in the wrist drop that results from paralysis of the musculo-spiral nerve...." These remarks might easily be misinterpreted (and they often are) as implying that such inability is a sign of *total* paralysis of the muscles referred to. This is, however, by no means necessarily the case; it merely shows that the muscles concerned are incapable of being concentrically contracted against the resistance to elongation of their antagonists, probably augmented by the pull of gravity which as a rule is never eliminated during the carrying out of such tests. Indeed it may be quite possible that if by means of posture or fixation gravity be first eliminated such concentric contraction may be demonstrable in the apparently totally paralysed muscles. And even if none can be thus obtained one is not justified in pronouncing a verdict of total paralysis until it has been proved that the muscles are quite incapable of excentric contraction. This is tested for by first passively performing the movement which the subject cannot perform unaided and then asking him to resist while the reverse movement (i.e. the return to the original position) is allowed to take place. Any retardation in the same as compared to its rate when the subject makes no such efforts is a proof of excentric contraction in the muscles that cannot as yet contract concentrically<sup>2</sup>.

Examples of all the foregoing might be multiplied to an almost indefinite extent, but those that I have given I think are sufficient to show what an important part the pull of gravity plays in movements of joints and how it can modify muscular activity and change concentric into excentric contraction. In conclusion I beg to express the hope that the power of excentric contraction will receive due appreciation and be accorded its correct place in text-books on anatomy, clinical medicine and neurology.

<sup>1</sup> What I have said above might at first sight give the impression that I consider that excentric contraction of muscles only takes place when it becomes necessary to antagonize the power of gravity which would if unopposed induce any given movement. This is of course not the case, as apart from the external agency of gravity, it is well known that the internal agency of concentric muscle contraction can induce it. Every such contraction is invariably accompanied by its antagonist allowing its tonic contraction to be overcome, or in other words by going through excentric regulating relaxation. The degree of excentric contraction in the latter case is however very much smaller than in the former case where the force of gravity has to be counter-acted and regulated.

<sup>2</sup> For further details see the author in *Brit. Journ. Child. Dis.* xi. 155-167, 1914.

## THE SYMINGTON PRIZE IN ANATOMY

PROFESSOR JOHNSON SYMINGTON, M.D., F.R.C.S. (ED.), LL.D., F.R.S., retired from the Chair of Anatomy in Queen's University, Belfast, in 1917. This is not the place to record the value of Professor Symington's work for Queen's University, it is sufficient to say that it is written in permanent records there; and in some measure was recognised when he was given the honorary degree of LL.D. It was considered, however, among his friends, that a memorial to Professor Symington which would characterise his own work should be founded by the University. A committee was appointed to consider the means to be adopted and instituted the "Symington Memorial Fund." Subscriptions to the fund were soon obtained, many of them, it is a pleasure to note, coming from those in all parts of the kingdom who had been associated with Professor Symington in his work; and it was resolved to found a Prize in Anatomy to be styled "THE SYMINGTON PRIZE," the committee believing that this would be a worthy memorial to him and one which would be to his own liking.

The "SYMINGTON PRIZE" in Anatomy of Queen's University of Belfast is now founded. It is the accumulated income of the Symington Memorial Fund. It is to be awarded every three years and for the first award will be of the value of about £30. The nomination to the prize rests with the Council of the Anatomical Society of Great Britain and Ireland and is to be made by the Council, entirely in its discretion, on the published results of research in Anatomy during the preceding three years. The prize is open to all junior anatomists who are members of the Anatomical Society of Great Britain and Ireland; holders of professorial rank are debarred.

It will give great pleasure to those who know him to learn how closely these arrangements agree with Professor Symington's own wishes and how pleased he is that there is in the award of the Society, of which he has been so long an active member, a prize for the encouragement of research among junior anatomists and which it must be so great a distinction to win.

The Prize has been awarded for the first time this year (1923) and the Council have nominated Dr Appleton, Cambridge University, and Dr Blair, Glasgow University, as the holders.

The next award will be made in 1926 when the value of the Prize will be about £40.

## REVIEWS

*Cunningham's Text-book of Anatomy.* Edited by ARTHUR ROBINSON, M.D., F.R.C.S. (Ed.). The Oxford Medical Publications. Henry Frowde and Hodder & Stoughton, London.

Twenty years have elapsed since the first appearance of this well-known text-book and little need be said in commendation of a work whose merits have been so exhaustively tested during that period by thousands of students and teachers all over the world.

"Daniel Johannes Cunningham adhuc loquitur"—this volume could have no more apt introduction, for, however changed the instruments, the vocalisation remains the same.

Naturally, the duties devolving upon the modern contributors are those of emendation and addition; these duties have been most worthily carried out by Professor J. T. Wilson who has re-written the article on the ductless glands, by Professor T. B. Johnston who has amongst other things greatly improved the article on the fasciae of the pelvis, by Professor S. E. Whitnall who has given us some very precise diagrams and especially by Dr E. B. Jamieson whose clear cut diagrams of many of the bones will be very welcome to the student. At the same time Professor T. Elliot Smith has made important alterations in his valuable article on the nervous system, more particularly as regards the cerebellum; while the editor, Professor A. Robinson, has incorporated most of the important results of recent investigation in his article on the development of the vascular system.

These are some of the more outstanding features of the present edition which is, and no higher praise can be bestowed upon it, a worthy successor of its predecessors.

Whatever Cunningham's text-book has to offer it may be said that, like every so-called text-book of anatomy, it fails in its objective since it caters for too wide a circle of readers. It demands the audience of the student, of the teacher and of the practitioner simultaneously. It would fulfil, at one and the same time, the functions of a text-book and of a reference book—candidly, it achieves neither.

Unfortunately anatomy, like every other observational and descriptive science, proceeds from data to generalisation and consequently the *Euclid of Anatomy*—the book which will proceed in logical, orderly and reasoned fashion from generalisations and principles to the facts and conclusions of structure (histological, embryological and macroscopical)—will be forthcoming in the distant future. Meantime many more steps than have been attempted hitherto



could be made toward this laudable ideal, and this to the great advantage of the student in particular—if a little more of the poetry and a little less of the prose of our science were tolerated in our text-books.

R. A. D.

*The Anatomy of the Human Orbit and Accessory Organs of Vision.* By S. ERNEST WHITNALL, McGill University. The Oxford Medical Publications: London.

When Professor Whitnall was at Oxford with Professor Arthur Thomson—to whom he inscribes this volume—it fell to his lot to give lectures to candidates for the Oxford Diploma of Ophthalmology, and these lectures afford the basis upon which the book is founded. It is, however, much more than a mere collection of lectures, being in reality a full work of reference on the subject with which it deals. The author has enlarged the scope of his work to include the neighbouring accessory sinuses of the nose and the cerebral connections of the orbital nerves. He has also described exhaustively all the structures lying within the four walls of the bony orbit and outside the eye itself: in fact, the only structure that he appears to have omitted as unworthy of remark would seem to be the *vena centralis posterior*.

The illustrations are numerous and good. One may not be enamoured with photographs as media for portraying dissections of soft parts, but good use is made of them in this book. Perhaps, in future editions, Professor Whitnall may see good to modify one or two of the schemes dealing with motor nerves to the orbit; as they stand they might conceivably afford the ignorant some ground for saying that these nerves in general emerge from the pons.

As stated above, the work is to be regarded as a book of reference, since the author seems to have extracted tribute from nearly everybody who has written anything on the orbit, or its contents, within relatively recent years; further, he has given a most extensive bibliographical list. Yet the book is no dry association of authorities under headings, but a well-written and most interesting series of descriptions of the several subjects of which it treats, and is in every way a volume which should have a recognised place in any anatomical library. The production is of the high standard that we are accustomed to find in the Oxford Medical Publications, and Professor Whitnall and all concerned are to be congratulated on the appearance of the work.

J. E. S. F.

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JOURNAL OF ANATOMY

CAMBRIDGE UNIVERSITY PRESS

LONDON: FETTER LANE, E.C. 4



H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1

WHELDON & WESLEY, LTD., 2-4, ARTHUR STREET, NEW OXFORD  
STREET, LONDON, W.C. 2

CHICAGO: THE UNIVERSITY OF CHICAGO PRESS  
(Agent for the United States and Canada)

BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.

TOKYO: THE MARUZEN-KABUSHIKI-KAISHA

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# JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF  
ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY  
OF GREAT BRITAIN AND IRELAND BY

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PROFESSOR J. P. HILL	UNIVERSITY OF LONDON
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LINCOLN'S-INN-FIELDS, LONDON, W.C. 2	

VOLUME LVIII

OCTOBER 1923—JULY 1924

CAMBRIDGE  
AT THE UNIVERSITY PRESS

1924

PRINTED IN GREAT BRITAIN

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## A HUMAN EMBRYO WITH HEAD-PROCESS AND COMMENCING ARCHENTERIC CANAL

BY THE LATE PROFESSOR PETER THOMPSON, M.D.,  
*University of Birmingham; Fellow of King's College, London,*  
AND JAMES C. BRASH, M.A., M.D., B.Sc.,  
*Professor of Anatomy, University of Birmingham*<sup>1</sup>.

TOWARDS the end of the third or beginning of the fourth week, and immediately preceding the formation of the neural groove, the human embryo passes through a phase of development characterised by the presence of certain axial structures, viz. the primitive streak, a head-process canalised by a rudimentary archenteric canal, and the notochordal plate. Even to-day but few examples of this stage are on record, and Grosser, who has published an interesting account of a young human ovum which showed these structures with great clearness, claims that previous to 1913—the date of his own publication—a similar stage of development in man had not previously been recorded. In 1918 Ingalls published an account of a human embryo, somewhat less advanced in development, but strikingly like the preceding in all the essentials. A third example was recorded by Strahl in 1916, but up to the present<sup>2</sup> the publication does not appear to have reached this country. Ingalls refers to it very briefly, and states that it shows a very similar stage of development, and adds that no data are given as to the age of the specimen.

The present paper is a further contribution to the subject, and, as far as can be ascertained, these four specimens comprise the material which illustrates a phase of development in the human embryo which falls somewhere between that represented by the ova of Fetzner, von Herff and Beneke on the one hand, and that represented by the ova of Frassi and Eternod and Graf Spee's Gle on the other. Estimating the age from the stage of development, Grosser gives 18 days, which is perhaps not far out. This archenteric stage, if such a term may be used for convenience, appears to be quite a transient one, and this may account for the small number of specimens which up to the present have been described.

The stage appears to correspond very closely with that which Wilson and Hill have described in their well-known work on monotreme development as the "post-gastrular stage." They point out that this stage "includes the de-

<sup>1</sup> The clinical history of this embryo was detailed by the late Professor Thompson in his Ingleby Lecture before the University of Birmingham, in October, 1918. The first part of this paper, including the "General description of the Ovum," he left in MS., and it represents all that he was able to complete for publication before his lamented death.—J. C. B.

<sup>2</sup> This was written in 1920.—J. C. B.

velopment, from the primitive knot, of the so-called 'head-process' together with various other phenomena associated with this, either causally or contemporaneously. This phase of development is deserving of special recognition," they say, "as constituting a new era, for, with its onset, the process of 'notogenesis' is initiated, and the proper axis of the future embryo (Minot's 'primitive axis') is laid down." A full description of the axial structures in our embryo will be given at a later stage. In the first place it will be more convenient to set forth the details of the clinical history, which have been obtained with great care and are practically complete.

#### CLINICAL HISTORY, ETC.

The ovum was removed from the uterus of a married lady by Mr Beckwith Whitehouse, F.R.C.S., on account of the serious condition of the patient's health. It came into my hands on the following day, intact, and enclosed within a capsule of decidua. The following notes taken by Mr Whitehouse accompanied the specimen.

The patient, Mrs X, was seen in consultation on December 3rd, 1917. She was of a neurotic and highly sensitive disposition, and had suffered from nephroptosis, for which she had consulted a surgeon a short time previously with a view to an operation for its relief. Pregnancy, however, had supervened, and this fact, together with the knowledge of the pending operation, produced an exacerbation of the mental symptoms, and suicidal tendencies were exhibited. After full consultation it was decided to explore the cavity of the uterus and terminate pregnancy if such really existed.

The catamenial history had previously been quite regular—menstrual cycle 28 days. The last period began on October 25, 1917, and ended on November 1. No menstrual period occurred as expected on November 22. The husband, who had been away from home, returned on November 2, and coitus took place on the evening of November 6. Mr X left Birmingham on the morning of November 7, and no further coitus occurred. (The coitus previous to that of the evening of November 6 took place some time before October 23, the day on which the husband left on a business journey for South Wales, but how long before is uncertain. That no coitus took place between these two dates, i.e. October 23 and November 6, forces us to the conclusion that a previous cohabitation may be definitely rejected as a possible factor in the case.)

Three days later, i.e. on November 9, the patient complained of pains in the breast, and thought that she was pregnant.

On December 3, upon examination under an anaesthetic, the body of the uterus was found to be somewhat globular in shape and very slightly enlarged. No softening of the cervix or other sign of pregnancy was present. However, taking into consideration the very slight increase in size of the organ, it was thought that a pregnancy might be present, and the uterine cavity was explored at 4.30 p.m.

The cervix was dilated by means of Hegar's dilators, and a blunt curette was introduced into the cavity of the organ. Presupposing that the ovum was situated either at the fundus or on the posterior wall, curettage of this area was performed first. A small ovum was removed intact from the posterior wall and placed immediately in a 10 per cent. solution of formalin. No chorionic villi were observed, and the ovum appeared as a small disc-shaped vesicle about half an inch in its greatest diameter. A small quantity of decidual tissue was also removed by means of the curette from the anterior and lateral walls of the uterus. The cavity of the organ was then packed with gauze.

From a perusal of the medical history given above, and from data supplied to Mr Whitehouse and myself by the patient and her husband, both of whom realised the importance of exact statement, it seems certain that fertilisation must have taken place after and was presumably effected by coitus on the night November 6-7, 1917. It should be stated that the husband of Mrs X is a well-educated man occupying a professional position in the commercial life of Birmingham, and the history detailed above can, in my judgment, be implicitly relied upon.

#### THE AGE OF THE SPECIMEN

Before entering upon a description of the embryo and its adnexa, something must be said regarding that most difficult problem, the age of the specimen. In our case we are in the fortunate position of knowing most of the essential facts, and yet the difficulties of arriving at a trustworthy conclusion within narrow limits are practically insuperable. Without a knowledge of such essential facts, the estimation of age is mere guesswork; with them we shall at least be able to arrive at an approximate estimate.

Moreover, from the standpoint of the history of the case, it is difficult to see how, under the circumstances, any additional or more reliable data could have been obtained, which would enable us to calculate the age with complete confidence. The really vital unknown factor is the day of the menstrual cycle on which the ovum was set free, and the absence of this knowledge is the barrier which hinders us in working out the problem with any degree of exactness.

The ovum was obtained thirty-nine days from the beginning of the last period, thirty-two days from the end of the period, eleven days from the omitted period, and twenty-seven (nearly) complete days after cohabitation. Assuming that an ovum was awaiting fertilisation, and allowing twenty-four hours for its occurrence, the absolute maximum time occupied by development was twenty-five or twenty-six days.

The fertilising coitus took place on the thirteenth day of the menstrual cycle, and sixteen days before the next expected but missed period. These days may well have been taken up by fertilisation, time consumed in travelling down the tube, the inhibition of menstruation, and the early stages of imbedding. In that case the ovum would reach the mucous membrane of the uterus



towards the end of the menstrual cycle, that is to say, at a period well adapted to its nutritional requirements.

This leaves about twelve days from the time of the imbedding of the ovum to the termination of pregnancy by operation on December 3. Bryce and Teacher allowed seven days after implantation for the further growth and development of the young ovum described by them in 1908, and considering that our ovum is much more advanced in development, the additional five days seems a reasonable allowance.

But are the assumptions which we have had to make regarding ovulation and fertilisation justified in the present case? Certain considerations, which must next be advanced, seem to show that they are not, and that a period of six or seven days must be deducted if, on the ground of the degree of development, we assign our ovum to its appropriate place in the third week of the chronological tables of young ova compiled by Bryce and Teacher, Keibel and Mall, and Grosser. For, as everyone admits, it is necessary, in attempting to ascertain the age of a young ovum, to consider factors other than those available in the obstetrical history of the case, and particularly the stage of development reached. Age and stage of development by no means always run parallel. For example, Keibel found in the pig differences which he regarded as equal to twenty-four to forty-eight hours' growth at such an early date as the fourteenth day of pregnancy. Nevertheless, any marked discrepancy between the stage of development and the estimated age demands careful scrutiny.

Now the stage of development in the ovum under discussion approximates to that found in the ova of Grosser and Ingalls, both of which have been estimated to be eighteen or nineteen days old, and is undoubtedly earlier than that shown by the ova of Frassi, Eternod, Delporte and Graf Spee's Gle, all of which have been placed at the end of the third week (nineteen to twenty-one days). True, amongst the six cases just noted, two only (Eternod's and Delporte's) have a clinical history comparable as regards fullness of detail with our specimen, but if, on the ground of the clinical history, it be maintained that ours is about a week older than the stage of development suggests, then a place in the fourth week in the chronological tables mentioned above, in company with His's Lg. and BB., would be incongruous.

Further, if the age of our ovum be estimated at eighteen to nineteen days on the ground of anatomical findings, then fertilisation occurred on the twentieth to the twenty-second day of the previous menstrual month. Such a date would harmonise with the observations of Fränkel on ovulation, which, based on one hundred and thirty-three laparotomies, go to show that ovulation occurs in the second half of the intermenstrual period, i.e. between the eleven to twenty-six days from the beginning of the last menstrual period, with an average of eighteen or nineteen days. In other words, ovulation would have occurred about one week after the fertilising coitus of November 6.

This would call for a sojourn of the spermatozoa in the Fallopian Tube of at least a week, a period during which it is reasonable to suppose they can

retain their fertilising power. Triepel has adopted a method of estimating the age of embryos based on the work of Fränkel, which consists of subtracting eighteen from the number of days reckoned from the beginning of the last period to the day when the ovum is obtained from the uterus. In our case,  $39 - 18 = 21$  days, which is quite a good result.

It will now be advantageous if we place here for purpose of comparison the essential points in the histories of the three ova most closely related to our own:

**FRASSI'S OVUM.** This ovum was obtained at an operation for total extirpation of the uterus on account of persistent menorrhagia due to metritis, forty-two days from the beginning of the last menstruation. Triepel estimates the age as  $42 - 18 = 24$  days; Bryce and Teacher estimate the age to be eighteen or nineteen days; Frassi himself describes it as being less than ten days, whilst the age reckoned on the basis of the stage of development is nineteen days. Such a result is a striking commentary on the danger of trying to narrow down too sharply the age of very young ova.

**INGALL'S OVUM.** This ovum was obtained thirty-four days from the beginning of the last menstrual period, as an abortion. Intercourse took place fourteen days previous to the abortion, and (doubtfully) also two weeks further back. Triepel's method would give an age of about sixteen days, whilst the age on the basis of development would be nineteen days. Ingalls himself estimates the age at seventeen or eighteen days, but he states that he could not bring himself to look upon this figure with any degree of confidence.

**GROSSER'S OVUM (KL. 13).** This ovum is younger than that of Frassi, and according to Triepel's method the age works out at eighteen or nineteen days. It was obtained as an abortion from a healthy uterus after an operation for removal of an ovarian cyst, thirty-seven days from the beginning of the last menstrual period. Owing to the irregularity of the menstrual cycle in this case, any estimate of age based on Triepel's method is likely to be misleading.

Therefore, from a perusal of these cases and others, one comes to the conclusion that the estimation of the age of young ova, now assigned to the third week, is a matter of approximation only, and it may be that in the future the age of some of them may have to be raised several days. For the present we must not be dogmatic. We shall go further and do more good if we strongly emphasise the approximate nature of our results. The problem under consideration is not one which can be solved with mathematical exactness, or by experiment, or by presentation of the unbroken chain of connected evidence.

To sum up, the main points in connection with the age of our ovum are:

(1) The stage of development, which would indicate an age of eighteen or nineteen days. This estimate must be very uncertain on account of the variability of time taken in travelling down the tube. According to Grosser, the error may, in extreme cases, be as much as four or five days.

(2) The obstetrical history, which gives a maximum time of development of twenty-five or twenty-six days. If, however, an interval of some days

occurred between insemination and ovulation, then this figure is correspondingly reduced, and (1) and (2) are brought more into harmony.

(3) A slow journey down the tube, which might add several days to an ovum apparently eighteen or nineteen days old. So that if insemination and ovulation coincided and fertilisation took place forthwith, the ovum may be the maximum age, viz. twenty-five or twenty-six days. In this connection it may be pointed out that Grosser estimates the tube journey to be fourteen days at least under normal conditions, and at other times perhaps twenty days.

Between a probable minimum age of eighteen or nineteen days and a maximum age of twenty-five or twenty-six days is a period of seven days—an interval of uncertainty. For the present, therefore, we must assign the ovum to the end of the third or to the early part of the fourth week of development.

#### GENERAL DESCRIPTION OF THE OVUM

The specimen lay in 10 per cent. formol for two days, and was then transferred to 60 per cent. alcohol, then 70 per cent. and then 80 per cent., when it seemed to be in a satisfactory condition for examination.

The ovum was enclosed in an envelope of decidua on which no scar could be detected. In shape it was rounded, flattened and lenticular (not unlike an ordinary tabloid, but not quite so flattened), and it measured  $13 \times 11 \times 8$  mm. On dissecting away the outer capsule of decidua, which separated quite easily, the chorionic vesicle with well-marked villi was exposed. When completely separated the vesicle measured  $10 \times 7.5 \times 4$  mm., so that the decidual capsule was from 1.5 to 2 mm. in thickness. On opening the vesicle, which was filled with a light-greyish mucin-like substance—the magma reticulare—a very small elongated papilla, attached by one extremity only, was found, the rest of the papilla projecting into the cavity of the ovum and connected by strands to the magma. The projection measured in spirit and before imbedding in paraffin about 2 mm. in length and about 1 mm. in breadth at its widest part. It must be pointed out that these measurements are probably too great, since one dare not touch the specimen with the dividers in case it should suffer some damage. Much time was spent in trying to obtain a photograph without any satisfactory result, and finally a freehand drawing was made with the assistance of the stereoscopic dissecting microscope at a magnification of 15 diameters (fig. 1). By these means the amnion, yolk-sac and body-stalk were brought clearly into view, together with the prominent caudal projection of the embryo-anlage, all these points being fully confirmed by subsequent examination of the serial sections. The drawing shows in addition the characteristic elevations or knobs on the yolk-sac, representing the angioblast, some villi (which measured 1 to 1.5 mm. in length) projecting from the outer surface of the chorion, and some maternal blood, also on the outer surface of the chorion and visible through the thin chorionic layer.

The projection with a small piece of the chorion to which it was attached was stained in bulk, borax-carminé being used. It was cut by Professor Carlier,



to whom I am much indebted for the trouble he has taken to obtain a good series of sections. Though not coming up to ideal requirements (some of the sections are broken owing to somewhat imperfect preservation), I was able to make a reconstruction in wax which turned out to be exceedingly useful as a means of interpreting certain obscure grooves on the embryo-anlage, and for settling beyond doubt the line of the axial structures. The bulk of



Fig. 1. The "Embryonic Papilla" attached by the body-stalk to the chorion. From a freehand drawing by Mrs P. Thompson.  $\times$  about 40.

the sections are quite satisfactory for study, and this is indeed fortunate, seeing that the combination of circumstances, which brings such a rare specimen, with a really good history, into the hands of an investigator, occurs so seldom. Altogether, reckoning from the cranial end of the embryonic shield to the blind end of the allantois, there are eighty-five sections. As the sections were each 10 microns thick, this gives a length of the shield *plus* allantois of .85 mm. From the cranial end of the yolk-sac to the attachment of the body-stalk to the chorion, the length estimated for the number of sections is 1.12 mm.

#### THE EMBRYO AND ADNEXA

The embryonic vesicle is similar in general form to that of Graf Spee's well-known Glaevecke ovum: the main features are shown in the drawing in fig. 1 already described and in the diagrammatic figs. 2 and 3. The embryonic shield, though it is a good deal broader in proportion to its length, more nearly resembles that of the Frassi ovum; but there is no neurenteric canal and the irregular ridges which are present do not appear to bound a neural groove.

There is a well-defined caudal projection or tail-fold and a less well-defined head-fold. The shield is  $\cdot 68$  mm. in length measured from the cranial reflection of the amnion to the caudal projection, and the estimated length including the caudal fold is nearly  $\cdot 9$  mm. The greatest breadth, which is found a little in front of the middle of the shield, is also about  $\cdot 9$  mm. In association with the ill-defined head-fold there is apparent evidence of the commencing forma-

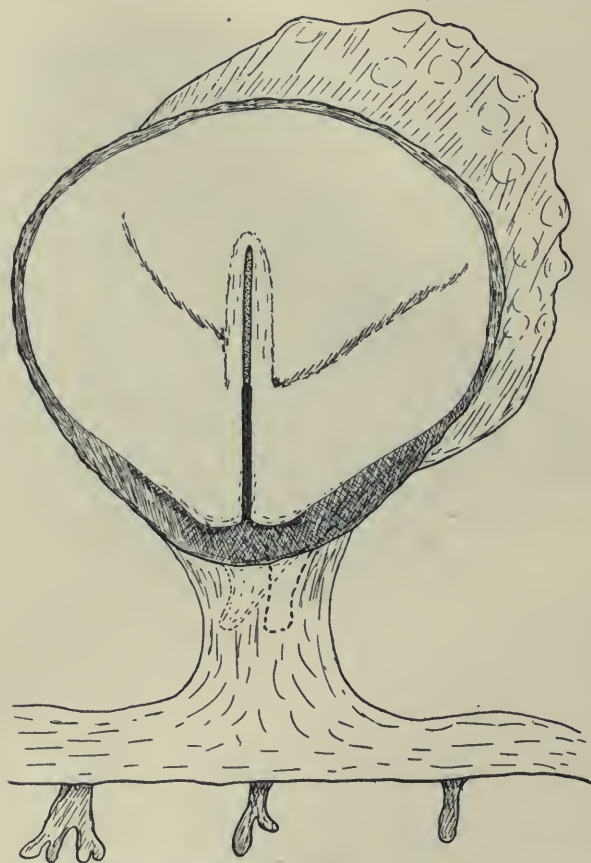


Fig. 2. Diagrammatic reconstruction of the embryonic shield, etc., to show the relation of the primitive streak, the median elevation and the two lateral grooves. The position of the head-process is indicated by a stippled band extending forward from the cranial end of the primitive streak beneath the median elevation. The relation of the amnion and the allantois to the body-stalk is also indicated. Drawn to scale,  $\times$  about 80.

tion of a foregut, cut separately from the yolk-sac in five sections; but, as there is in this region some distortion of the vesicle with collapse and infolding of the amnion and yolk-sac, it remains doubtful whether the foregut appearance is to be attributed to these causes.

The irregular ridges which are present on the shield, somewhat similar to the ridges on the shield of the embryo about the same stage of development

described by Ingalls, have provided rather a difficult problem; their relation to the axis of the embryo is not at first sight obvious. It was to elucidate this point that Professor Thomson made the reconstruction to which he refers. I know that he did not look upon the resulting model as completely satisfactory, and there is no doubt that it cannot be taken as an exact representation of the original. This is due to the absence of guide lines, a serious handicap when it is realised that the sections are oblique to both the median plane and to the surface of the shield; in addition there is evident distortion of a number of the sections. The model itself is unfinished, and as it was never intended to

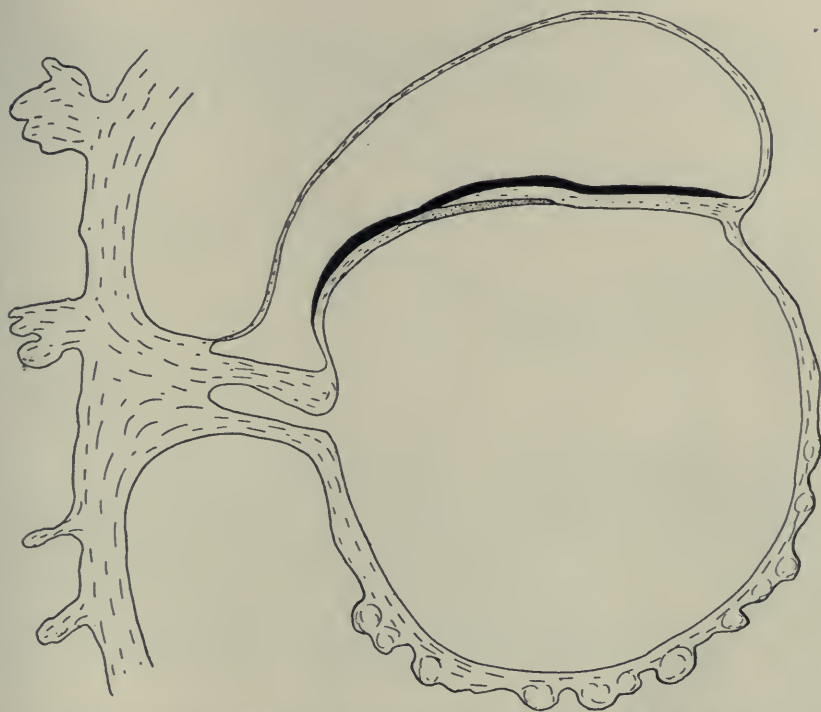


Fig. 3. Diagrammatic median sagittal section; the head-process, etc., as in fig. 2. Drawn to scale,  $\times$  about 80.

be more than an incidental help in interpretation of the appearances of the sections and an aid in settling the question of the middle line, I do not feel justified in reproducing it. I prefer to use it, as was Professor Thompson's intention, along with a close study of the sections themselves, in order to reconstruct diagrammatic representations of the surface of the shield and of an ideal median sagittal section of the ovum.

#### THE SURFACE OF THE SHIELD

The reconstruction of the surface of the shield is given in fig. 2, which is drawn carefully to scale. In general shape the dorsal aspect of the shield is



oval with its long axis transverse to the long axis of the embryo. The cranial end of the shield is represented by one side of the oval and is bent slightly downwards; the caudal end of the shield appears as a narrowing prolongation of the other side of the oval; it is markedly bent downwards and the projection thus formed is indented in the middle line by the primitive groove. The groove becomes shallower as it is traced forwards to end, a little less than one-third of the distance from the caudal projection to the cranial end of the shield, at the point where the median elevation and the right depression next to be described commence. The whole length of the primitive groove is estimated to be .38 mm.

Immediately in front of the anterior end of the groove there commences a median elevation of the shield in the position usually assigned to Hensen's knot. This elevation, accentuated by the obliquity of the sections and in addition rendered very prominent by the presence on each side of a depression or groove, extends forwards on the shield for a distance a little greater than that occupied by the primitive groove, and reaches therefore about the junction of the anterior and middle thirds of the shield. On each side of the median elevation is a groove, narrow behind but broadening in front; these grooves are about the same length. The left commences at the middle of the median elevation, extends forwards and to the left and fades away in the cranial half of the shield without quite reaching its edge. The right begins at the hinder end of the median ridge, where it forms a deep depression immediately to the right of the anterior end of the primitive groove, and extends to the lateral edge of the shield about its middle. The interpretation of these ridges depends upon a study of the axial structures in section.

#### THE AXIAL STRUCTURES

Fig. 4 is from a section a little in front of the middle of the cranial half of the shield. It demonstrates the general structure of the shield and shows that the ectoderm and the entoderm are in this region separated by a small amount of (primary?) mesoderm. There is here no indication of a neural groove. The sections in this region are believed to be practically vertical to the surface of the shield, as is evidenced by the single layer of nuclei in the entoderm and the amniotic ectoderm. The embryonic ectoderm, on the other hand, shows a stratification of its nuclei, two and in some places three deep, and, as the three-layered nuclei are mostly confined to an area on each side of the middle line, it is possible that we see here the commencing formation of the neural plate. Close to the entoderm in the middle line are to be seen a few mesoderm-like cells in the position where the head-process is situated further back. These cells, however, do not constitute a forward continuation of the head-process as the same region of the entoderm is a continuous single layer both in front of and behind this particular section. It is to be noted that there is in fact no evidence in the cranial part of the shield of a "completion plate" continuing

the line of the head-process forward. We pass now to the caudal end of the shield.

Fig. 5 is taken from a section a little in front of the middle of that part of the primitive streak which appears on the dorsal aspect of the shield, i.e. in front of the caudal bend. Here is to be observed the continuity of the three



Fig. 4. Transverse section about the middle of the cranial half of the shield.  $\times 95$ .

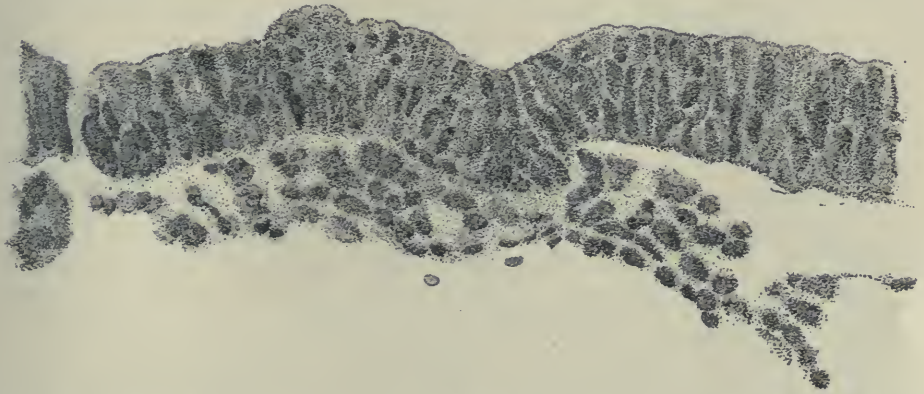


Fig. 5. Transverse section of the primitive streak region in front of the caudal bend; description in the text.  $\times 385$ .

layers, but there is by no means complete fusion. The entoderm is somewhat damaged on the left, but it passes as a continuous thin layer from side to side closely united to, though quite distinct from, the mesoderm. The ectoderm, which is relatively independent, is thickened in the middle line where the nuclei are three and four deep; here also are to be observed the primitive groove indenting the surface, and, corresponding to this, a ridge-like depression of the ectoderm towards the entoderm. It is from the anterior end of this

ridge that the head-process appears to take origin. Behind the region of this section the streak becomes progressively thinner until, when a point a little beyond the caudal bend is reached, it becomes reduced to a single layer of entoderm and ectoderm in apposition in the region of a cloacal membrane. The position of the cloacal membrane is indicated in fig. 3, but, owing to the great obliquity of the sections to the surface in this region, it is hardly possible to determine its exact extent. We now turn to the head-process itself and the relation which it presents to the anterior end of the primitive streak.

Now about the point where the primitive groove, as seen in fig. 5, gives place to the median ridge already mentioned and seen in the next section figured, i.e. in the position assigned to Hensen's knot, there is the appearance of a downgrowth of a wedge of cells from the ectoderm in direct continuity with the ridge beneath the primitive groove. This apparent downgrowth is clearly marked four or five sections behind the most anterior showing the primitive groove, and is the result of the sectioning of a column of cells which is found to continue the line of the primitive streak forwards between the ectoderm and the entoderm. Its centre appears at first to be slightly to the left of the anterior end of the primitive streak, but as it passes forward it lies directly beneath the median ridge of the shield. It is in continuity behind with the ectoderm at the anterior end of the streak as stated, and it maintains the same relation to the mesoderm as is exhibited by the primitive streak itself. Traced forward it begins at once to separate from the ectoderm and is from its origin in contact with the entoderm; in the course of eight or nine sections it is entirely free from the former and closely united to the latter.

A section at the most favourable point (figs. 6 and 7) makes clear the general relations of the column, which is thus identified as a head-process. The figures also show that although there is no distinct lumen present yet the dorsal cells are arranged fanwise as if the lumen were about to appear. The section figured is situated fifteen sections in front of the origin of the process from the ectoderm of the knot and fourteen sections behind its cranial termination: the whole length of the head-process is estimated to be nearly  $\cdot 3$  mm. In front of the process the simple condition of the entoderm, as seen in fig. 4, appears at once, and, as already stated, there is no evidence of the formation of a "completion plate" continuing the line of the process forward. The thickening of the process is merely replaced by (primary?) mesoderm and the entoderm is unaffected. These topographical points are summed up in the shield diagram of fig. 2 and the schematic sagittal section of fig. 3, where the head-process is represented by a stippled band passing forward beneath the median elevation of the ectoderm and in continuity with the entoderm. There can be little doubt, judging from the absence of a definite canal and the manner in which the process ends in front, that we are dealing with an example of the head-process in course of formation, probably just before the appearance of a lumen and the breaking down of the ventral floor. There is no sign of perforation towards either the ectoderm or the entoderm, so that the stage is without doubt previous



to that of the notochordal or archenteric canal and *a fortiori* of the neurenteric canal.

The more highly magnified view of fig. 7 shows very clearly the arrange-



Fig. 6. Transverse section at the midpoint of the head-process showing the ridges and grooves on the shield and the relation of the head-process to the median elevation.  $\times 95$ .

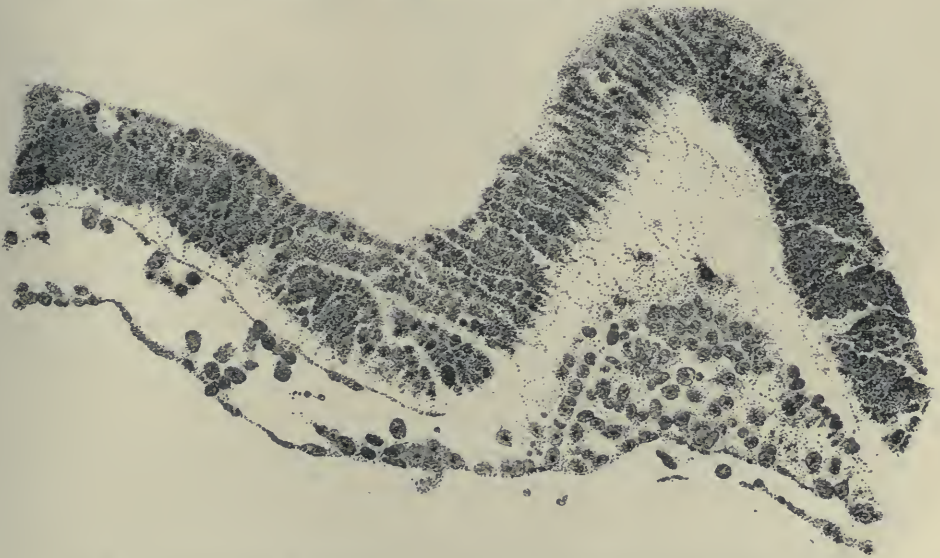


Fig. 7. Portion of the preceding,  $\times 300$ , showing the head-process in detail.

ment of the cells. The distinction between the ventral simple layer (plaque lécithoentérique of van Beneden) and the dorsal clump with its radial arrangement foreshadowing the canal (plaque notochordale of van Beneden) is indi-

cated both by the actual arrangement of the cells and by the staining reactions. These figures (6 and 7) also demonstrate that the line of the head-process corresponds to the line of the central elevation of the shield and that this is to be considered as indicating the axial line of the embryo. The appearance of thickening of the ectoderm along this ridge is probably largely due to the obliquity of the sections, which is also the case with the other two ridges

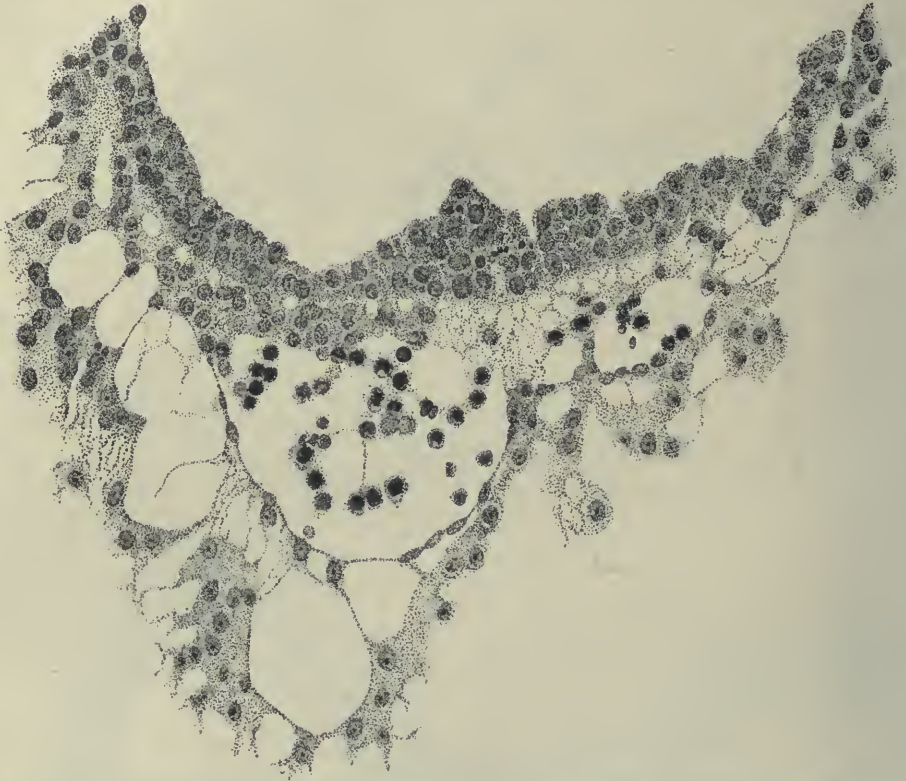


Fig. 8. The wall of the yolk-sac, near the cranial pole, showing blood-island.  $\times 385$ .

previously mentioned. All three ridges must be considered to be due to a folding of the surface of the shield, partly due to exuberant growth and partly artificial.

#### THE AMNION

The amniotic ectoderm consists of a single layer of flattened cells continuous with the peripheral two-celled embryonic ectoderm and backed by an equally thin mesodermic covering. The amniotic cavity is a good deal distorted in many of the sections, but there is no doubt that there is a greater depth of this space at the cranial than at the caudal end of the shield. In the region of the caudal bend the amnion appears to be stretched over the shield, and as this diminution of the cavity corresponds with the presence of the grooves on the shield, the impression that these grooves may be due to

an exuberant growth of the shield is somewhat strengthened. Traced backwards the amnion is found to bend in conformity with the caudal bend of the shield itself, and, with a slight convexity towards the deep depression between the shield and the body-stalk, it passes directly on to the dorsal aspect of the latter. It covers the stalk for about half its extent, and, as a result of the bend mentioned, the last few sections of the amnion appear as a narrow space lying on the left side of its dorsal aspect (figs. 3 and 10). There is no evidence of the presence of an amniotic duct, the amniotic ectoderm remaining histologically the same at the extremity of this small diverticulum as elsewhere, with no extension towards the chorion.

#### THE ENTODERMIC CAVITY

The median sagittal diagram of fig. 3 indicates clearly the conditions present. In five sections at the cranial end the lumen of the intraembryonic portion is cut separately from the yolk-sac cavity, but a doubt, accentuated by the obliquity of the sections, remains whether this is in reality foregut or due to a distortion of the wall of the yolk-sac. There appears, however, to be some thickening of the mesoderm, with a doubtful coelomic rudiment, in the angle between. The allantoic diverticulum extends from the dorsal part of the caudal wall of the yolk-sac into the body-stalk, which it traverses for rather more than half its length. The total length of the allantois is estimated to be .14 mm. There is no hindgut.

#### THE MESODERM

A thin layer of (primary?) mesoderm—mostly one cell thick—extends throughout the shield, while secondary mesoderm is in process of active formation in the primitive streak and is in continuity with the head-process in front, with the somatopleuric and splanchnopleuric layers, and with the chorionic mesoderm along the body-stalk. The chorionic mesoderm forms a continuous layer lining the chorionic ectoderm and extending into the primary villi.

#### ANGIOGENESIS

The distribution of the angioblastic tissue is, with doubtful exceptions in the body-stalk, confined to the wall of the yolk-sac. The evident blood-islands in this situation have already been noted in the general description of the ovum, and a detailed examination of the sections reveals that they are distributed thickly on the whole of the ventral aspect of the sac and extend on to both its cranial and caudal extremities. On the whole it appears that the islands in the cranial half of the sac are in a more advanced state of development. It is not proposed to give a detailed histological description of the appearances presented by these blood-islands, but attention may be directed to certain important features which are to be seen in the illustrations given.

It will be observed from fig. 4 that the entoderm for about the dorsal half of the wall of the yolk-sac consists of a single layer of cells, whereas in the



ventral half it is thickened so that there are two, three and in some places four and even five nuclei. It may be thought that this appearance is due to distortion and consequent obliquity of the sections, but a careful examination of all the sections reveals that this is the condition throughout the extent of the yolk-sac. Associated with this difference it is found that, whereas in the dorsal half of the yolk-sac the overlying mesoderm is separated from the entoderm by a distinct space and is clearly independent of it, in the ventral area there is no such clear separation between the two. Here also the mesoderm is thickened and the blood-islands occur. The separation of the yolk-sac into two areas, a dorsal and a ventral characterised by the differences in the entoderm mentioned, was described by Minot, and in Streeter's account of a human embryo (Mateer) of the presomite period the same separation of the mesoderm from the entoderm in the dorsal half of the sac is noted. In that embryo, however, which, in a younger stage than the present specimen, exhibits a much less differentiated condition of the yolk-sac blood-anlage, it is the ventral part of the mesoderm which is thinner and "fused tightly with the entoderm." The significance of these observations must lie in their relation to the formation of the blood vessels and the blood cells.

If we now examine the blood islands themselves we find that there are all intermediate stages present between the extremes of small clumps of cells lying between apparently simple entodermic and mesodermic layers and completely formed vessels with uninterrupted endothelial walls containing the developing blood cells. The three main stages are illustrated in fig. 4, where from left to right are to be seen (1) clumps of cells between entoderm and mesoderm each single-layered, (2) partially formed vessels with endothelial wall unformed towards the thickened entoderm, and (3) a fully formed vessel. The middle of these stages is illustrated on a larger scale in fig. 8, taken from a different section nearer the cranial pole of the yolk-sac. This section shows the formation of the endothelial wall on the side of the island away from the entoderm and the characteristic relation of the blood cells to the entoderm, from which they appear to hang in a cluster into the lumen of the developing vessel. In fig. 9, on a still larger scale, is shown the portion of the entoderm with which these cells are apparently continuous. It will be observed from this figure that the cells from which the clump in the lumen apparently springs are differentiated from the cells next the cavity of the sac by a number of points. There is the same absence of cell outlines throughout, but the cytoplasm surrounding the nuclei in the deeper layer is more clearly differentiated, the outlines of the nuclei are less regular, the nuclei are more deeply stained, and the layer as a whole is separated from that next the cavity by a row of spaces. It is clear that these cells are to be separated from the overlying entoderm, and that between the two layers will be formed the completion of the endothelial wall. Although the appearances here described are at first sight suggestive of the origin of the blood cells from the entoderm, yet there is no unequivocal evidence to warrant a conclusion on this difficult question.

It should be noted that there are great variations in the distribution of the vessels in embryos about this stage of development. The contrast, for example, between this ovum and Streeter's Mateer specimen is very marked. In the latter, blood vessels are present in all parts of the chorion and in many of the

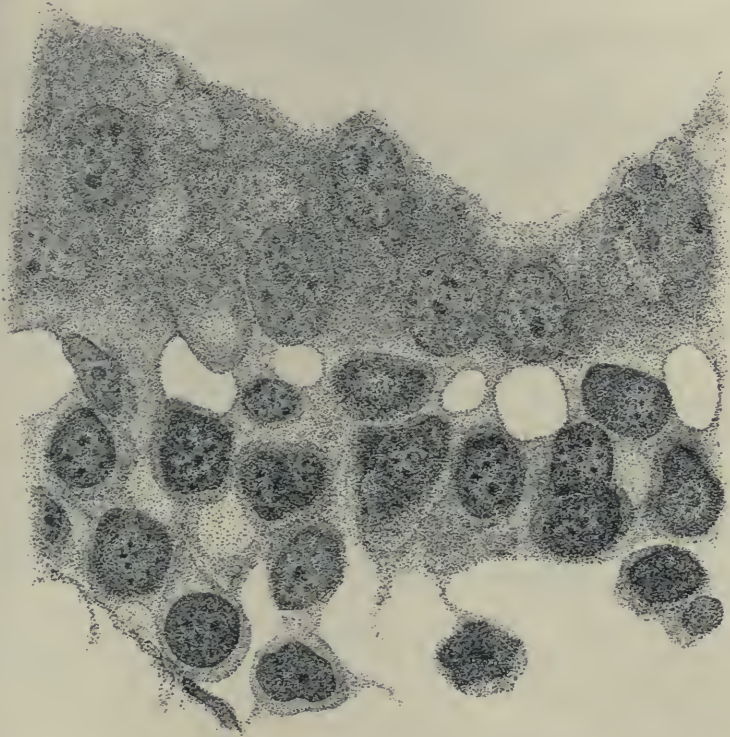


Fig. 9. Portion of the preceding (the left upper corner of the island) to show the arrangement of the cells on the yolk-sac side of the island.  $\times 1750$ .

villi, while the differentiation of the vessels on the yolk-sac is restricted to the caudo-ventral half and has not advanced so far as in the Whitehouse specimen.

#### THE COELOM

There is no indication of an intraembryonic coelom with the exception of a doubtful space in the mesoderm between the cranial wall of the yolk-sac and the doubtful foregut. Elsewhere the intraembryonic mesoderm is almost entirely one cell thick. There is no special remark to make regarding the exocoelom, beyond calling attention to the statement in the general description that there was a considerable quantity of magma present, to which the embryonic papilla was connected by strands.

## THE BODY-STALK

The structure of the body-stalk is illustrated in fig. 10, in which is to be seen the allantois in the centre of the lower part of the stalk and, on the side,



Fig. 10. Section of the chorion and the body-stalk, showing the allantois in the centre and the amniotic diverticulum on the side of the stalk.  $\times 95$ .

a section of the amniotic diverticulum which passes along the stalk for a short distance. It will be noted that the mesoderm immediately surrounding the allantois is more compact than that which is connected with the chorion.

## THE CHORION AND VILLI

Figs. 11 and 12 are added, without detailed comment, to demonstrate the structure of the chorionic wall and the villi. It may be noted that the distribution of the villi is very irregular, that the cyto- and plasmodi-trophoblast layers are everywhere very distinct, and that the cores of the villi consist exclusively of undifferentiated mesoblast, in most cases shrunken away from the walls in preparation. There is no sign anywhere of vascularisation.

## SUMMARY

1. There is an excellent clinical history, by means of which the age of the ovum can be placed between a minimum of eighteen or nineteen and a maximum of twenty-five or twenty-six days.
2. The head-process is in course of formation, and the stage of development is probably just before the appearance of the archenteric canal and the breaking down of the lecitioenteric plate.
3. The amnion is stretched over the caudal end of the shield and is con-



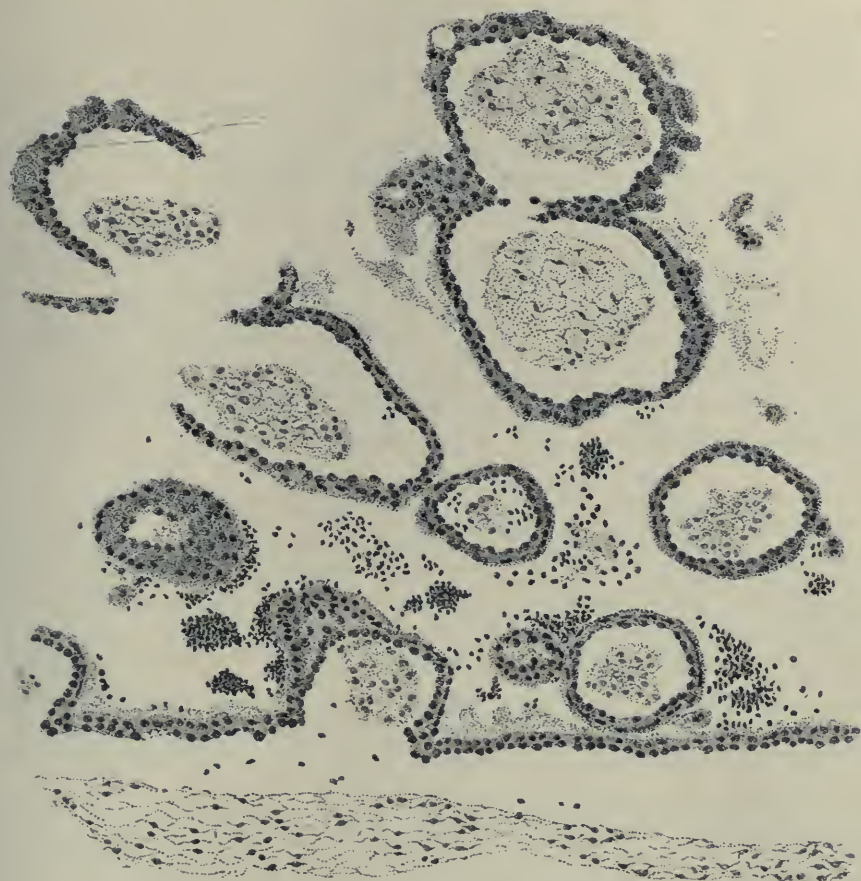


Fig. 11. Chorion and villi.  $\times 142$ ,

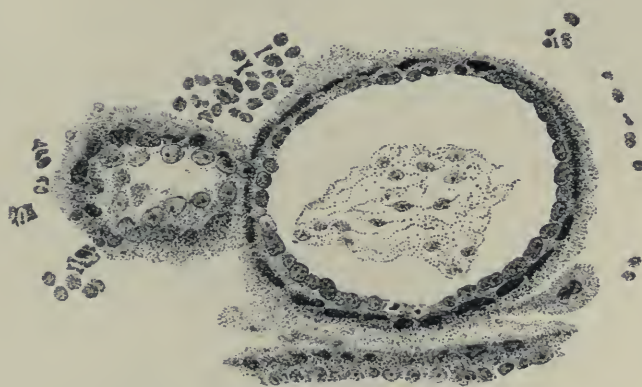


Fig. 12. Portion of the preceding.  $\times 350$ .

tinued as a short diverticulum on the dorsal and left side of the body-stalk. There is no evidence of an amniotic duct.

4. There is a doubtful foregut, no hindgut, and an allantoic diverticulum of the yolk-sac extending about half-way along the stalk.

5. Blood and blood vessel formation is restricted to the ventral wall of the yolk-sac and is slightly more advanced towards the cranial end.

6. There is no intraembryonic coelom.

In conclusion I have to thank Mrs Thompson for her ready assent to the proposal that the work begun by her late husband should be completed, and for her kindness in placing at my disposal his unfinished MS. and notes. Also I have to acknowledge my indebtedness to Professor Barelay-Smith for his advice and to Professor Arthur Robinson for his kindness in looking over the material at my disposal and for helpful suggestions.

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# THE EFFECTS OF X-RAYS UPON THE SKIN OF THE FROG TADPOLE

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The expenses of this research were defrayed by a grant from the Medical Research Council.

THE object of the experiments described in the following paper was to ascertain the effects of prolonged irradiation upon rapidly growing tissue at different periods after exposure, and also to see in what manner these effects are modified by irradiation in the presence of colloidal silver. In the latter case, not only are the effects produced due to the action of the primary beam but also to the soft secondary radiations given off from the minute colloidal particles of the metal.

For the purpose of experiment frog tadpoles were used; these were exposed to the unscreened radiations from a Coolidge tube working at 2 milliampères with a 7-inch spark gap. In most of the experiments the animals were exposed in  $1\frac{1}{2}$  inches of water in open glass dishes, the distance of the anticathode of the tube being  $6\frac{1}{2}$  inches from the surface of the water. As the tadpoles tended to lie at the bottom of the vessel it is clear that there must have been a certain amount of "screening" from the superjacent layer of water. In order to diminish this factor, other specimens were exposed for different periods in about  $\frac{1}{2}$  inch of water, the water being changed from time to time (every 20 minutes) during the exposure, so as to eliminate as far as possible any heating effects. The distance of the anticathode from the surface of the water was, as before,  $6\frac{1}{2}$  inches. In a further series a small amount (.04 per cent.) of protargol was added to the water containing the tadpoles, in these cases the irradiation was carried out in dishes containing  $1\frac{1}{2}$  inches of protargol mixture; the distance of the anticathode being again  $6\frac{1}{2}$  inches. The specimens examined may be considered as falling into seven series:

*Series A.* Normal tadpole skin.

*Series B.* Tadpoles irradiated immediately after death.

*Series C.* Living specimens irradiated in  $1\frac{1}{2}$  inches of water for  $1\frac{1}{2}$  hours. Different specimens taken and killed after varying intervals.

*Series D.* Specimens irradiated for 2 hours in  $1\frac{1}{2}$  inches of water, individuals killed and examined as in Series C.



*Series E.* Specimens irradiated for 5 hours in  $1\frac{1}{2}$  inches and examined as before.

*Series F.* Specimens irradiated for 5 hours in about  $\frac{1}{2}$  inch of water.

*Series G.* Specimens irradiated in the presence of protargol.

#### SERIES "A"

##### NORMAL TADPOLE SKIN

As is seen in fig. 1, the epidermis consists of only two layers of cells. Of these the superficial layer is formed of somewhat flattened cells with more or

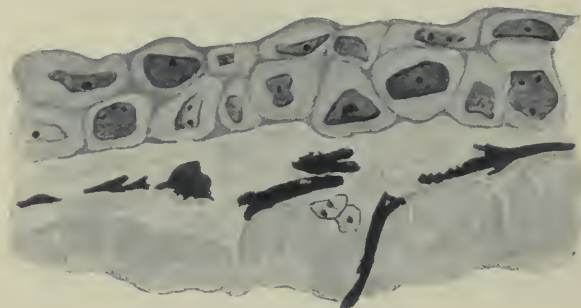


Fig. 1

less oval nuclei; while in the deep layer the cells tend to become polygonal in outline and the nuclei roughly correspond to the shape of the cell.

As regards their staining properties, a great variation is noted in the affinity of the nuclei for the stain, though generally speaking the nuclei in the basal layer stain more deeply than do those in the superficial layer. This may possibly be due to the fact that the paler nuclei are also the smaller and that they are contained in smaller cells, hence the amount of nucleoplasm is smaller and the depth of colour not so great.

Chromosomes are never seen distinctly, but nucleoli are generally particularly well marked. The cytoplasm stains well and exhibits a somewhat clearer area immediately surrounding the nucleus, but no granules or fibrils are present. The cell outlines are extraordinarily well defined and present many of the appearances of typical cell walls, even to marked thickenings in the angles between contiguous cells. If there are any intervening lymph channels, they are not demonstrable in any specimen examined. The corium varies greatly in depth, but it is never so wide as to exceed the width of the epidermis. Its structure is not very obvious, since generally it stains as a homogeneous pink mass, although a feltwork of white fibrous tissue and a network of elastic fibres can be indistinctly seen. In addition there are also present a few cells which are oval or polygonal in form; the polygonal cells give off fibrils and their nuclei are large with well-defined nucleoli.

It is, however, the pigment cells which form the most characteristic feature of the corium. These lie deeply and in close apposition to the subjacent muscle

bundles; they vary greatly in size and shape and are generally markedly arborescent. Comparatively few of them penetrate between the muscle bundles and none are seen between the epidermal cells. They are extremely friable and small masses of pigment are often seen scattered over the whole area of a section. That this appearance is due to rupture of the pigment cells during the various processes of preparation and cutting may be assumed from the fact that these scattered granules are in all cases very small and that they may be seen apparently lying in the lumen of the gut as well as superimposed on all tissues, when a section through the whole body is examined.

In cases where more gross injury has occurred, it is seen that the epidermis is torn away as a whole, while the corium together with its pigment cells remains attached to the deeper structures.

#### SERIES "B"

##### TADPOLES IRRADIATED FOR $1\frac{1}{2}$ HOURS IMMEDIATELY AFTER DEATH

Here the superficial layer of epithelium appears more flattened than in the preceding series, but it is possible that this is due to a general shrinking which is noticeable in all the epidermal cells. The nuclei stain deeply; in some cases they show a little indistinctness of outline and in certain instances are broken up, the fragments being scattered throughout the whole of the cell. In the great majority of cases, however, the nuclei are intact and lie in the centre of the cell with the cytoplasm adherent to them so that it seems to be torn away from the periphery with the production of a marginal clear space. These appearances are presented by the epidermal cells of both layers; the chromosome filaments are more distinctly seen than in Series "A" while, on the other hand, the nucleoli are less obvious. No changes can be detected in the corium and its pigment cells.

#### SERIES "C"

##### TADPOLES IRRADIATED FOR $1\frac{1}{2}$ HOURS AND KILLED AT DIFFERENT TIMES AFTERWARDS

The third series of sections was taken from tadpoles which were irradiated for a period of  $1\frac{1}{2}$  hours. Different specimens were taken and killed at varying intervals after exposure, while a few that died are also included in this Group C.

##### C 1. *Specimens killed immediately after $1\frac{1}{2}$ hours' irradiation*

The epidermis shows no change except in a few localised areas in the thinnest part of the tail, where the cells are larger and the nuclei more active-looking. No definite hyperplasia can be seen in any part of the section.

In the corium the pigment cells are less branched than normal and are collected into clumps.

##### C 2. *Specimens killed 24 hours after $1\frac{1}{2}$ hours' irradiation*

Many small areas show very active nuclear division with local loss of definition of the cell outline. The nuclei seem rather smaller than normal,

when considered in relation to the size of the epithelial cells. Nucleoli are distinct and taken in conjunction with the shape of the nuclei, serve to indicate early mitosis.

Although this is active in these localised areas, there is no definite increase in the thickness of the epithelium, nor is there any invasion of the corium by epithelial cells. The outstanding feature in these specimens is, however, the



Fig. 2

fact that all distinction between superficial and basal layers is completely lost (fig. 2).

The corium exhibits no deviation from the normal except that the pigment cells have withdrawn their amoeboid processes and shrunk into rounded masses lying deep in the true skin.

*C 3. Specimen died 27½ hours after 1½ hours' irradiation*

The epithelial nuclei all stain deeply with the exception of those present in one part of the skin, which must be described in greater detail.

In this area the nuclei show great activity, exhibit marked variations in size and take up the haematoxylin stain rather faintly; the nucleoli stand out distinctly. Many nuclei are in a state of active division although the mitotic figures are not distinct. The cell outlines are no longer distinct in the particular area though they remain definite elsewhere. The most striking and important phenomenon exhibited in this part of the section is the loss of demarcation, not only between the cells of the epithelium—which now practically amounts to a syncytium—but between this area and the corium. This active layer is seen to be invading the deeper part of the skin by gradually merging into it. There are no definite downgrowths of cells but the appearances suggest an encroaching wave of the hyperplastic area (fig. 3).

In the corium the nuclei of the connective tissue cells stain deeply, but the pigment cells in the great majority of cases lie deeply in the epidermal syncytium and are markedly arborescent.

*C 4. Specimens killed 48 hours after 1½ hours' irradiation*

The epithelial nuclei are all large and have distinct nucleoli; in many cases they are markedly granular and there is some surrounding vacuolation of the cytoplasm, an appearance presented equally by both layers of cells.



There are numerous areas of hyperplasia in which the distinction between superficial and basal cells is lost, with the result that the epithelium presents marked variations in thickness. In addition to this there are many areas where invasion into the corium has occurred both by a local syncytium and by individual epithelial cells, many of which can be seen lying in the corium, some

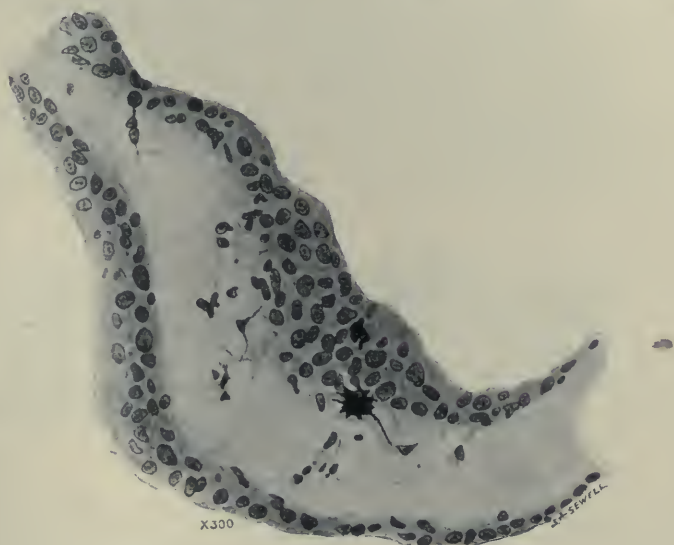


Fig. 3

of them very deeply. There are more patches of hyperplasia than have hitherto been manifested, and while each of these areas shows less indication of cell division than is present in the preceding group (C 3), it is more marked than in group C 2. There are a few small clumps of pigment cells in the hyperplastic area of the epidermis, but by far the greater number lie deeply in the corium and are markedly arborescent.

No other changes are noticeable in the corium.

*C 5. Specimens killed 84 hours after 1½ hours' irradiation*

The corium and chromophores in this series of tadpoles present appearances identical with those observed in the previous series (C 4). The epithelium, however, shows more marked hyperplasia and for the first time exfoliation of many new superficial cells can be detected. These are small in size and consist of a nucleus surrounded by only a very thin layer of cytoplasm. Although all the nuclei are distinct and healthy looking—no single sign of degenerative change can be seen—they give the general impression of being smaller and less active than those seen in the last group (C 4).

*C 6. Specimens which died 7 days after 1½ hours' irradiation*

In these specimens the epidermis is represented merely by a wavy line with but few small local thickenings, and all details of structure are com-

pletely lost. This line consists of an evenly stained strip which has taken up eosin and haematoxylin equally, so that it appears as a thin lilac thread, which is very friable and easily detached from the subjacent tissue.

The corium presents an appearance similar to that shown by the epithelium, with the exception that in a few places small patches of striation can be made out. Also there are one or two spheroidal cells, with an indefinite histological structure apart from their very distinct outline. They stain a deep blue and appear to consist almost entirely of nuclear substance.

At first sight there appears to be a remarkable diminution of pigment, but higher magnification demonstrates an absolute fragmentation of the pigment cells, and a dispersal of pigment granules throughout the whole of the corium, which is filled with minute brown particles (fig. 4).

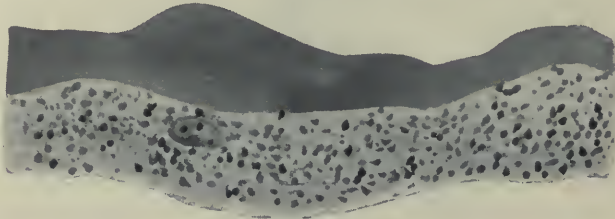


Fig. 4

A very striking feature of this (Series C) and the foregoing series B, is the extremely patchy distribution of the areas of hyperplasia.

#### SERIES "D"

##### TADPOLES IRRADIATED FOR 2 HOURS

###### D 1. *Specimens killed immediately after 2 hours' irradiation*

There is a slight but very definite hyperplasia in places, but the cell outlines are quite distinct and there is no attempt at syncytium formation. Some separation has occurred between many of the basal cells, with the result that the cell outlines are extraordinarily distinct and a definite space intervenes between the adjacent cells. Perinuclear vacuolation can be seen in many cells both of the superficial and of the deeper epithelial layers, while the nuclei themselves are deeply and evenly stained, clearly defined and somewhat shrunken. Nucleoli are difficult to detect. Pigment is seen to lie as a narrow band, parallel to the epithelium and deep in the corium, while a few pigment cell masses lie deep in the connective tissue where there is also an apparent increase in the cellular elements.

###### D 2. *Specimens killed 24 hours after 2 hours' irradiation*

In this series the basal epithelial cells show hyperplasia with some syncytium formation and very definite invasion of the corium in a few places (fig. 5). In these situations the nuclei are smaller than usual, more deeply

stained and more crowded. Deep in the epidermis there occur a few collections of cells of similar structure which are quite separated from their fellows in

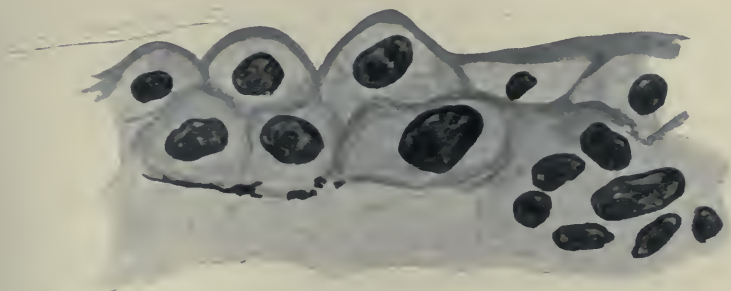


Fig. 5

the epithelium. The nuclei are similar to those seen in the preceding series (D 1), but perinuclear vacuolation is here more marked.

In the corium the pigment cells appear as rounded masses lying superficially, the fibrous strands are more clearly seen in the deeper layers where the connective tissue cells show a patchy but distinct increase in numbers.

#### SERIES "E"

##### TADPOLES IRRADIATED FOR 5 HOURS AND KILLED AT DIFFERENT TIMES AFTERWARDS

###### E 1. *Specimens killed immediately after 5 hours' irradiation*

In these it is seen that there are one or two patches of epithelial hyperplasia chiefly affecting the basal cells but showing no tendency to invasion of the corium. In general the cell outlines are less distinct than normal, many cells are vacuolated while a few exhibit no signs of any nuclear staining at all. Here the nuclei are probably entirely degenerated, a hypothesis supported by the fact that a small number of definitely fragmented nuclei are found in adjacent cells. The great majority of the nuclei are smaller than normal and show marked variations in the degree to which the haematoxylin is taken up.

The pigment cells immediately below the basal layer are medium sized horizontal masses and show little tendency to arborescence. There are no other apparent changes in the corium.

###### E 2. *Specimens killed 24 hours after 5 hours' irradiation*

Most striking is the fact that in these preparations by far the greater part of the epidermis is narrow, shrunk and attenuated. All differentiation between superficial and basal layers is lost and the cell outlines are no longer distinct; the nuclei are small but stain well. There are, however, a few stretches of epithelium—averaging about four cells in length—which show complete absence of nuclei, a homogeneous stretch of protoplasm serving to represent the whole epithelial structure.



Hyperplasia has evidently occurred in a few places and although these areas are wider than the rest of the epithelium, even they are somewhat shrunken.

In contrast to this general picture of attenuation are some small areas where the cells are larger than normal. They are, however, apparently oedematous and the condition is really one of cloudy swelling.

The corium shows no definite change, with the exception that the chromophores, which lie immediately under the epithelium are rounded and show no tendency to arborisation.

#### *E 3. Specimens killed 48 hours after 5 hours' irradiation*

In these specimens, while there are a few areas in the epithelium in which hyperplasia has occurred and is still occurring, the general picture is one of degeneration. The epithelium is narrowed and although there are no extensive areas which show an absence of nuclei there are many small patches from which they have disappeared. Many nuclei are crenated and degenerate and many are fragmented, while numerous cells show signs of breaking up. The appearances presented by the pigment cells are the same as those in the previous series (E 2).

#### *E 4. Specimens killed 72 hours after 5 hours' irradiation*

Here the picture of neighbouring hyperactivity and degeneration is most obvious. Many large stretches of basal cells show a homogeneous protoplasm, complete loss of cell outline and but a few scattered nuclei. Other small patches of epithelium are thinner and generally resemble the preceding except for the fact that the nuclei are few and far between and apparently remain like memorial stones to indicate where the cells have been. Immediately adjacent to these areas are basal cells with active nuclei and exhibiting hyperplasia. In these spots, however, the overlying flattened cells appear to be oedematous and show the first stages of degeneration (fig. 6). The nuclei exhibit marked

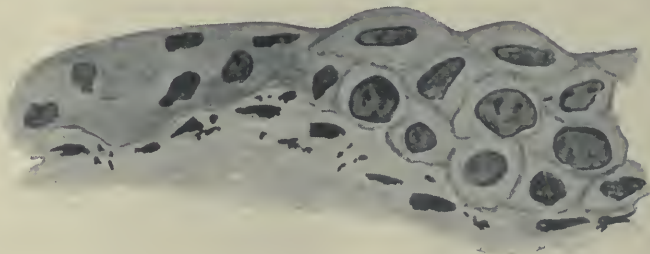


Fig. 6

variations even in contiguous cells, thus degenerated and fragmented specimens are immediately contrasted with their large and active fellows. Indeed, some of these large nuclei are the largest observed throughout these experiments, being larger than the nucleus of a normal cell.

The pigment cells are somewhat fragmented and the smaller masses appear lighter in colour than usual, this is, however, probably an optical effect due to the shorter diameter of the clumps.

E 5. *Specimens killed 96 hours after 5 hours' irradiation*

In these sections the whole epithelium is degenerated; in many cases a thin apparently structureless thread is all that remains, but occasionally a few living basal nuclei can be seen. Much of the pigment is still present in the medium sized irregular masses adherent to the epithelial remains. Upon examining the section with a higher power, however, it soon becomes evident that the whole of the corium is bestrewn with minute light brown specks evidently resulting from the fragmentation of some of the chromophores.

In all the preceding experiments the tadpoles had been irradiated in about  $1\frac{1}{2}$  inches of water, the surface of the water being 6 inches from the anode of the X-ray tube. In the series now to be described, the depth of water was reduced to  $\frac{1}{2}$  inch, in order to reduce screening effects from the depth of water, the distance of the anode from the surface of the water being 6 inches, as before. In this group (F) 5 hours' irradiation was given. The water was frequently changed during the exposures.

SERIES "F"

TADPOLES IRRADIATED FOR 5 HOURS IN ABOUT  $\frac{1}{2}$  INCH OF WATER  
AND KILLED AT DIFFERENT TIMES AFTERWARDS

F 1. *Specimens killed immediately after 5 hours' irradiation  
in about  $\frac{1}{2}$  inch of water*

The epithelium shows one or two hyperplastic patches, no degenerative changes are seen, and some of the nuclei appear somewhat smaller than normal. The cells, however, are very distinctly outlined and in some places are separated from one another. This phenomenon is in all probability due to a loosening of the epithelial cells and not to the presence of lymph channels as the spaces are too large and there are no intercellular fibrillæ.

The pigment is collected into large spheroidal clumps and very few arborescent figures are seen.

Now, for the first time, among all the specimens examined, we meet with definite changes in the corium as the result of irradiation. The fibrous tissue is broken up, the elastic fibres are short and twisted, giving a picture resembling on a small scale the appearance presented by a hair affected with ringworm fungus.

No changes are seen in the connective tissue cells.

F 2. *Specimens killed 24 hours after 5 hours' irradiation  
in  $\frac{1}{2}$  inch of water*

The epithelium is very friable and easily detached from the corium and shows a few small patches of hyperplasia. Most of the nuclei stain but faintly

and all are small; in some places they are degenerated or dead and occasionally fragmentation and dispersion through the cytoplasm have occurred.

The appearances of the corium and the chromophores are the same as in the preceding series (F 1).

F 3. *Specimens killed 48 hours after 5 hours' irradiation  
in  $\frac{1}{2}$  inch of water*

For the most part the epithelial cells are shrunk and narrowed and the protoplasm is contracted down on to the nuclei. Large swollen cells with very pale and indistinct nuclei are present in patches, they are very friable and have generally lost immediate connection with one another, thus causing a break in the epithelial continuity. Apparently these represent dying areas of hyperplasia, and are the result of degeneration occurring in such over-developments as were seen in series F 1.

When the cytoplasm is closely contracted around the nuclei, the latter are small and often scarcely distinguishable from the rest of the cell.

The connective tissue is torn away from the basal layer of the epithelium and the bundles of white fibrous tissue are all swollen and œdematous. The same fate has overtaken the connective tissue cells which are mostly large and spherical with pale indistinct nuclei; the others are shrunk and round with complete absence of all processes. There is complete fragmentation of the pigment cells with distribution of small pigment granules throughout the corium.

SERIES "G"

TADPOLES IRRADIATED FOR 2 HOURS IN THE PRESENCE OF PROTARGOL

This series consists of tadpoles which had been irradiated in water to which 1 per cent. of a solution of protargol had been added. After exposure to the rays the larvæ were transferred to ordinary pond water.

G 1. *Specimens put into the protargol for 2 hours, then removed  
and killed immediately*

These were not subjected to any irradiation, but were used merely as controls to determine whether simple immersion in the dilute colloidal silver were productive of any changes in the skin. On microscopical examination these sections exhibit no deviation from the normal, with the exception that they seem abnormally friable and that the chromophores appear as rounded or oval masses in the corium and show little or no tendency to branching.

G 2. *Specimens killed immediately after 2 hours' irradiation  
in dilute protargol*

All the cells are seen to be small and shrunk, but in spite of this there are signs of commencing hyperplasia both in the epithelium and in the connective tissue. The whole of each section is very fragmented and certainly much more so than in the control series (G 1). This effect may be in part due



to the action of the protargol apart from irradiation as the same picture is noticed in all the tadpoles which have been simply immersed in the colloidal silver solution. The pigment is distributed in the same manner as in the control series, but with the difference that the chromophores are not quite so large or so ovoid and there is certainly more branching of the cells.

G 3. *Specimens killed 48 hours after 2 hours' irradiation  
in dilute protargol*

Hyperplasia of the epithelial cells is more marked in these specimens than in any hitherto described. On an average the epithelium is increased to five cells in thickness. A further important point is that this hyperactivity is uniformly distributed over the whole of the skin and is not present merely in

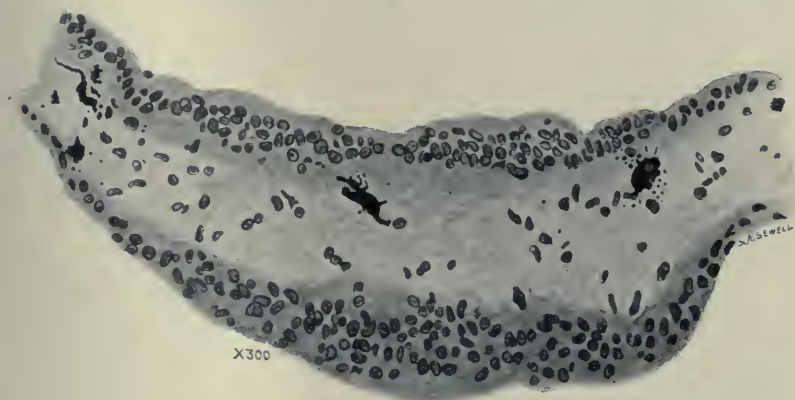


Fig. 7

patches. Cell outlines are frequently indistinguishable, and the whole section is very friable. The same activity is seen in the connective tissue cells of the corium which also show a marked tendency to branching. The pigment is contained in small and markedly arborescent cells (fig. 7).

The results obtained may be tabulated as follows:

Series	Experiment	Nuclei	Epithelium	Corium	Pigment cells	Remarks
A	Normal	Large. No chromo- somes seen. Nucleoli often clear. Smaller nuclei stain less in- tensely than do the larger	An outer layer of flat- tened cells and an inner basal layer more cuboidal in shape. Clear cyto- plasm. No fibrils.	Generally stains as a homogeneous pink mass. Here and there both types of fibres can be seen. A few oval and poly- gonal cells	Lie deeply in corium. Mostly arborescent. Vary in size. None between epithelial cells and few between muscle bundles. Very fri- able	Picture is remarkably constant (fig. 1)
B	Irradiated for $1\frac{1}{2}$ hours after death. $6\frac{1}{2}$ inches from anode	Less definite in outline. Often broken up. Stain deeply. Nucle- oli less obvious	All cells shrunken. Cy- toplasm torn from cell wall and ad- herent to nuclei	No change	No change	
C 1	Killed immediately after $1\frac{1}{2}$ hours' irra- diation. $6\frac{1}{2}$ inches from anode	In a few patches they are larger and more "active-looking"	In the same patches the cells are larger. No hyperplasia	No change	Less branched and rather clumped	That the few changes noted in the epi- thelium are defi- nitely the first signs of an increased ac- tivity of the cells, is borne out by the subsequent series
C 2	Killed 24 hours after $1\frac{1}{2}$ hours' irradiation. $6\frac{1}{2}$ inches from anode	Active division in many small areas. Nucleoli distinct and taken in conjunction with shape of nu- cleus indicate mito- sis although chromo- some filaments were not distinguishable	In these areas there is loss of cell outline. No increase in thick- ness of epithelium and no invasion of corium	No change	Complete withdrawal of pseudopodia. All rounded	Early but definite signs of epithelial hyperplasia. Mito- sis and loss of dis- tinction between external and basal layers in patches (fig. 2)

C 3	Death 27½ hours after 1½ hours' irradiation. 6½ inches from anode	In one part, there is great activity. Many faintly staining nuclei. Distinct nucleoli. Mitosis. Vary greatly in size. Elsewhere the nuclei stain more darkly	In this one area all suggestion of cell outline is lost. Practically a syncytium. Elsewhere cell walls are distinct. No downgrowths of cells into corium but a loss of distinction in this one patch	Nuclei stain darkly	A few rounded cells are superficial. Mostly deep and arborescent	One area shows marked hyperplasia and early invasion of corium, rather by means of an encroaching wave than by downgrowths of epithelial cells (fig. 3)
C 4	Killed 48 hours after 1½ hours' irradiation. 6½ inches from anode	All large and with distinct nucleoli. Many small areas of mitosis. Many granular and with surrounding vacuolation	Many areas where cell outlines are lost. Invasion of corium not only by means of syncytium but also by means of individual cells	No change	Mostly deep and very markedly arborescent	More patches of hyperplasia. More definite invasion of corium
C 5	Killed 84 hours after 1½ hours' irradiation. 6½ inches from anode	All distinct and healthy. No definite signs of degeneration but many seem smaller and less active in appearance. Otherwise as in C 4	Even more hyperplasia. Some exfoliation. Exfoliated cells are small and consist almost entirely of nucleus with but little cytoplasm. Invasion as in C 4	As in C 4	As in C 4	Hyperplasia of epithelium and invasion of corium. Exfoliation. A suggestion of early degeneration in many nuclei
C 6	Death 7 days after 1½ hours' irradiation. 6½ inches from anode	None seen	All structure lost	All structure lost. A few spheroidal cells left	Absolutely fragmented	Absolute degeneration (fig. 4)
D 1	Killed immediately after 2 hours' irradiation. 6½ inches from anode	Clearly defined. Deeply stained	Slight but definite hyperplasia in patches. No loss of cell outline. No invasion	No change	Mostly contracted into small masses. A few arborescent cells lie deeply	Very early epithelial hyperplasia
D 2	Killed 24 hours after 2 hours' irradiation. 6½ inches from anode	Nuclei as in D 1	Definite hyperplasia. Some syncytium formation. Definite invasion of corium	Fibrous strands distinct. A patchy but distinct increase in the cells	Superficial, rounded and clumped	Hyperplasia and invasion of corium (fig. 5)



Series	Experiment	Nuclei	Epithelium	Corium	Pigment cells	Remarks
E 1	Killed immediately after 5 hours' irradiation. $6\frac{1}{2}$ inches from anode	Mostly smaller than normal. Vary greatly in staining power. Same degeneration and fragmentation	Definite patches of hyperplasia but no invasion of corium. Many cells vacuolated and many apparently without nuclei	No change	Medium sized clumps and but few pseudopodia seen	Hyperplasia of epithelial cells. No invasion of corium. Concurrent early degeneration
E 2	Killed 24 hours after 5 hours' irradiation. $6\frac{1}{2}$ inches from anode	Mostly small and stain well. A few areas show complete absence of nuclei	All distinction between the two layers is lost. Cell walls lost, shrunken, narrow. A few cells large and show cloudy swelling. Hyperplasia has evidently occurred here and there	No change	Absolute absence of arborescence	Hyperplasia has evidently occurred but the picture is now one of degeneration
E 3	Killed 48 hours after 5 hours' irradiation. $6\frac{1}{2}$ inches from anode	A few in areas of hyperplasia look active. Many more crenated, fragmented and degenerate. Completely absent in many cells	Mostly narrow and degenerate. Many cells breaking up. A few patches of hyperplasia	No change	As in E 2	A few hyperplastic areas but the essential picture is one of degeneration
E 4	Killed 72 hours after 5 hours' irradiation. $6\frac{1}{2}$ inches from anode	Some definite areas of hyperplasia with active nuclei. Vary greatly in size. Many are degenerate and many absent	Many cell walls lost. Some cloudy swelling. Other patches show definite active hyperplasia	No change	More broken up and so each seems to be less dense	Degeneration and hyperplasia side by side, the former predominating and beginning to supervene in active areas (fig. 6)
E 5	Killed 96 hours after 5 hours' irradiation. $6\frac{1}{2}$ inches from anode	Degenerate	Degenerate with a few living basal cells left	No change	Some small clumps, but fragmentation is more complete and more general	Degeneration is now universal

F 1	Killed at once after 5 hours' irradiation. 6½ inches from anode. Shallow dish	Many small nuclei	A very few small hyperplastic areas. No invasion of corium	Fibrous tissue here seen to be definitely broken up. No change in the cells	Large spheroidal clumps	Very early hyperplasia
F 2	Killed 24 hours after 5 hours' irradiation. 6½ inches from anode. Shallow dish	Mostly small and faintly staining. Some definitely fragmented	Occasional patches of hyperplasia. Very friable	Occasional patches of hyperplasia. Very friable	As in F 1	As in F 1
F 3	Killed 48 hours after 5 hours' irradiation. 6½ inches from anode. Shallow dish	Often pale and indistinct. Many small and degenerate	Most cells shrunken, many show cloudy swelling and are separated from each other, particularly in the hyperplastic areas	White fibres swollen and cedematous. Cells show cloudy swelling. Many shrunken and degenerate. No processes	Complete fragmentation	Degeneration now general
G 1	Kept in protargol fluid for 2 hours and then killed	Normal	Normal	Normal	Normal	Normal
G 2	Killed at once after 2 hours' irradiation in the protargol fluid. 6½ inches from anode	All small	Cells small, but there is definite early hyperplasia	No change	More branching than in G 2	Very early hyperplasia
G 3	Killed 48 hours after 2 hours' irradiation in the protargol fluid. 6½ inches from anode	Active. No degeneration. No mitosis seen	Hyperplasia marked and general. No degeneration. Some detached cells in corium	Hyperactivity of cells	Extremely arborescent	Hyperactivity general and not restricted to small areas. No degeneration (fig. 7)

## CONCLUSIONS

The details of the experiments and the experimental findings have been so fully dealt with in the text and in the tabular summary that a note of conclusions seems rather a formality than a necessity.

In the specimens irradiated immediately after death (Series B), very slight changes were noticed; these nevertheless seem to have been due to the irradiation.

Prolonged irradiation within certain limits causes the characteristic changes to appear more quickly, for instance, a specimen killed immediately after  $1\frac{1}{2}$  hours' irradiation showed only some increase in the size of the nuclei of the superficial epidermal layer together with evidences of increased activity (C 1), while specimens which had received 2 hours' irradiation and which were killed immediately afterwards, showed slight but definite hyperplasia (D 1).

The chromophores in the corium appear to be very responsive to the rays.

Irradiation in the presence of colloidal silver causes much more rapid and profound changes. These were of a markedly stimulative character, within the limits of time after irradiation in which the observations were made.



# ARE THE POLAR AND TRABECULAR CARTILAGES OF VERTEBRATE EMBRYOS THE PHARYNGEAL ELEMENTS OF THE MANDIBULAR AND PREMANDIBULAR ARCHES?

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IT is, I believe, now generally accepted that the visceral clefts of the gnathostome vertebrates are intersegmental in position, and that the most anterior somite is the premandibular. Each somite of the region where these clefts occurred must accordingly have lain, primarily, directly dorsal to the related arch, and that part of the axial skeleton developed in relation to that somite must have lain directly dorsal to the skeletal bar developed in the arch. The presence of a premandibular somite strongly suggests a premandibular arch related to it, and there must inevitably have been such an arch if the present mouth has been developed from a pair of mandibular clefts.

The skeletal bars of all these arches, with the possible exception of the premandibular, must have lain, primarily, transverse to the axis of the body, and each of them must have lain directly internal to the artery of the related arch. They probably did not extend upwards as far as the longitudinal aortic vessel into which the efferent arteries fell, but had they extended to it, lying as they did internal to the efferent arteries, they would have passed internal (ventral) to it, as the second pharyngobranchials actually do in both *Amia* and *Hyodon* (Allis, 1897, fig. 55, Pl. 35 and 1919, fig. 7, Pl. 21).

In later stages of phylogenetic development, the arches became inclined to the axis of the body, and in the branchial region of the gnathostome fishes two distinctly different forms of arch arose, a sigma-shaped one, in which the pharyngobranchials project postero-mesially, and a V-shaped one, in which those elements of the arches project antero-mesially, the former form of arch being found in all of the recent Elasmobranchii, and the latter form in the Teleostomi and Dipnoi.

In the adults of the recent Selachii, where the sigma-shaped arch is found, the dorsal end of the epibranchial in each of the more anterior arches is somewhat expanded, the posterior corner of this end giving articulation to the pharyngobranchial, and the anterior corner projecting anteriorly beyond it, as is well shown in certain of Gegenbaur's (1872) figures. The efferent artery of each arch, coming upwards along the external surface of the epibranchial, accordingly either passes wholly anterior to the pharyngobranchial, or crosses its anterior edge, and beyond that point lies wholly anterior to it, as shown

in my figure of *Chlamydoselachus* (Allis, 1915, p. 568). Thus the dorsal ends of the pharyngobranchials of these fishes do not now lie directly internal to the efferent arteries of their respective arches, and if that part of the axial skeleton to which any one of them is related were to undergo marked lateral expansion, the skeletal bar of that arch would acquire contact with it dorsal to the dorsal aortic vessel, and would lie posterior to the efferent artery of the arch if the contact was by the pharyngeal element of the arch, but anterior to that artery if the contact was by the epal element. And this is exactly what does occur in the hyal arch of these fishes, for the hyomandibula, which is the epal element of the arch, articulates with the cranial wall dorsal to the lateral dorsal aorta and anterior to the efferent hyal artery (Allis, 1915). In the Batoidae, where the hyomandibula is the pharyngeal element of the hyal arch, it also articulates with the cranial wall dorsal to the lateral aorta, but its primary relations to the efferent hyal artery are obscured by its loss of contact with the dorsal end of the epal element.

In the Teleostomi, where the V-shaped arch occurs, the dorsal ends of the epibranchials are expanded, as they are in the Selachii, but it is the anterior, instead of the posterior, corner of this end that gives articulation to the pharyngobranchial; as shown in my figures of *Amia* and *Scomber* (Allis, 1897 and 1903). The dorsal end of the efferent artery of each arch of these fishes accordingly lies either wholly posterior to the pharyngobranchial, or crosses its posterior edge, the reverse of the relations that it has to that cartilage in the Selachii. If one of the branchial bars of these fishes were to acquire contact with a laterally expanded part of the axial skeleton, the point of contact would therefore lie anterior to the efferent artery of the arch and dorsal to the dorsal aortic vessel, and such contact is actually acquired by the first pharyngobranchials in *Amia*, *Scomber* and *Hyodon* (Allis, 1897, 1903 and 1919).

The relations of the arteries, here under consideration, to the cartilages of the hyal and branchial arches thus seem to depend definitely upon whether the skeletal bars of these arches acquire the sigma- or the V-shaped form, and whether their dorsal ends lie opposite an enlarged portion of the axial skeleton, or not, and this must have applied with equal force to the relations of these structures to each other in the mandibular and premandibular arches. In these two latter arches, the dorsal ends of the skeletal bars must inevitably, in all the gnathostome fishes, have assumed the sigma form, for, in all of them, as the present mouth developed, the pharyngeal elements must have been subjected to pressure, or pull, tending to swing them upwards and forwards into a position parallel to the axis of the body, while the articulating ends of the epal and ceratal elements were pushed backwards. It seems reasonable to assume that there was, primarily, an aortic vessel in the premandibular arch, as there actually is in the mandibular arch. The efferent artery of each of these arches would therefore, normally, have passed anterior to the pharyngeal element of the arch in order to reach and fall into the lateral dorsal aorta, and this latter vessel would have extended forwards to the dorsal end of the

premandibular artery. From this end of the aorta, the arteria cerebralis of current descriptions must have had its origin, for this is in accord with the conditions that I find in the adults of all of these fishes that I have examined, and with Raffaele's (1892) descriptions of embryos of the Plagiostomi.

Assuming the views above set forth to be correct, it is evident that, in recent fishes, the relations of the arteries here under consideration to the cartilages of the region, should give some indication as to whether the latter are of visceral (branchial), or axial origin, and the conditions in early embryos of *Acanthias*, as recently described by van Wijhe, are particularly suggestive in this respect.

In a 28 mm. embryo of this fish (*Acanthias*), the polar cartilage of either side is said by van Wijhe (1922) to be a little rectangular plate lying ventral to the parachordal of its side, slightly posterior to its anterior end and directed vertically toward it. The hind end of the corresponding trabecula is shown lying directly ventral to the polar cartilage, and it is said (*l.c.* p. 283) there to be in contact with the dorso-anterior end of the palatoquadrate. In the figures given, this contact of the trabecula and palatoquadrate is not shown, but as it is said to exist, the adjoining ends of these two cartilages must both lie directly ventral to the ventral end of the polar cartilage, and but slightly separated from it. The dorso-anterior end of the palatoquadrate is said to represent the palatobasal process of Gegenbaur's (1872) descriptions of the adult, but, following Garman (1885), van Wijhe calls it the processus palato-trabecularis. It is evidently considered by him to represent the dorsal end of the entire bar of the mandibular arch, but this I think is incorrect, as will later appear.

The polar cartilages enclose between them a space which van Wijhe calls the "Polfenster," and in this 28 mm. embryo it is said to be traversed by the stalk of the hypophysis and the internal carotid arteries. The latter arteries, running forwards through this fenestra polaris, unite with each other immediately beyond it and then soon separate again, the artery of either side turning laterally and being joined by the efferent pseudobranchial artery (arteria spiracularis, van Wijhe) shortly after the latter artery has given off the arteria ophthalmica magna. The internal carotid is said then to continue onwards, along the lateral surface of the hypophysis, and after giving off the arteria centralis retinae, to first turn upwards across the anterior edge of a median mass of tissue that van Wijhe calls the "Mittelhirnpolster," and then postero-mesially along the dorsal surface of that polster to join and fuse with the artery of the opposite side to form the median arteria basilaris.

The "Mittelhirnpolster" lies partly within and partly anterior to the ventro-posteriorly bent and beak-like tip of the notochord, and corresponds to the cartilago acrochordalis of certain other vertebrates. In *Acanthias* it does not undergo chondrification, but lateral outgrowths of it chondrify as the pleurospenoid (van Wijhe), or alisphenoid (Sewertzoff) cartilages, and as these latter cartilages and the acrochordalis tissue are said to be derived



from somite I, they form the most anterior portion of the chordal axial skeleton. The internal carotid of these descriptions accordingly does not enter the chordal portion of the cranial cavity until after it has received the efferent pseudobranchial artery and has given off the arteria centralis retinae, and as the internal carotid, up to the point where it receives the efferent pseudobranchial artery, is simply a section of the lateral dorsal aorta, it is evident that it must there have lain, primarily, external to the cranial cavity; and this is in accord with the conditions that I have described in the adult *Acanthias blainvillii*, in the adults of several others of the *Selachii*, and in *Raia* (Allis, 1914, 1912 a, 1912 b), the internal carotid there, after traversing the foramen caroticum and until it has received the efferent pseudobranchial artery, lying either in a canal in the cranial cartilage or between that cartilage and its lining membrane.

In embryos of *Acanthias* from 29.5 to 32.5 in length, the ventral end of each polar cartilage has fused with the hind end of the corresponding trabecula, but the dorsal end of the cartilage is still free.

In a 39.5 mm. embryo, the polar cartilages of opposite sides have fused with each other both dorsal and ventral to the median artery formed by the fusion of the internal carotids, a posterior portion of the fenestra polaris thus being cut out of the entire fenestra to form a foramen caroticum, and this foramen persists as such in the skull of the adult. That part of the fused polar cartilages that forms the dorsal boundary of this foramen has fused with the ventral surface of the parachordal plate; the parachordal, polar cartilage, and trabecula of either side thus forming a single continuous piece. The palatoquadrate has grown forwards beyond the point where the polar cartilage fuses with the trabecula, and a processus palatobasalis (palato-trabecularis, van Wijhe) has developed on its dorsal edge, this process being directed upwards along the lateral surface of the trabecula definitely anterior to the polar cartilage. A short palatine process of the palatoquadrate projects anteriorly beyond the processus palatobasalis. The internal carotids of opposite sides now fuse with each other before they enter the median foramen caroticum, and the ectodermal stalk of the hypophysis has vanished.

The efferent pseudobranchial artery of these descriptions is the efferent artery of the mandibular arch, and the internal carotid, into which it falls, is simply an anterior prolongation of the lateral dorsal aorta. This latter artery thus lies ventro-mesial to the polar cartilage, and the efferent mandibular artery, in order to reach it, crosses the anterior edge of the latter cartilage, these relations of the arteries to the cartilage being exactly those that the corresponding arteries in the branchial region would have to the pharyngeal elements of those arches if the latter elements were to acquire contact with the axial skeleton. This evidently suggests that the polar cartilage is a pharyngo-mandibular, and the further facts that this cartilage lies ventral to the jugular vein, lies ventral or posterior to all branches of the nervus trigeminus, and at a marked angle to the palatoquadrate, are all in favour of this view. The

fact that the polar cartilage develops independently of the palatoquadrate is in accord with van Wijhe's statement that the several cartilages in the more posterior arches of this fish develop independently of each other, instead of arising by the segmentation of a primarily continuous bar.

In embryos of *Scyllium canicula*, somewhat different but strictly comparable conditions occur. In the descriptions of embryos of this fish the polar cartilages are not described as independent cartilages, but it seems beyond all question that the so-called trabeculae of these descriptions are, in reality, trabeculo-polar cartilages. Goodrich (1918, p. 21) says of these so-called trabeculae: "At no stage of development do I find the trabeculae bent down at right angles to the parachordal plate, as figured by Sewertzoff, but always from the first more nearly in the same plane"; and van Wijhe (1922) confirms this observation. Goodrich, in making this statement, refers to his figure of a 33 mm. embryo, and the trabeculae, as there shown, do lie nearly in the plane of the parachordals, but they nevertheless lie nearly at right angles to that part of the notochord toward which they are directed, for the anterior end of the notochord turns upwards to such an extent that its tip lies nearly at right angles to its otic and occipital portions. The conditions in this fish are thus strictly comparable to those in *Acanthias*; and as I find similar relations of the cartilages of this region to the nerves, arteries and jugular vein in the adults of all of the *Selachii* that I have examined, and also in *Raia* (Allis, 1912b, p. 58) and *Chimaera* (Allis, 1917), it is probable that they exist in all the *Elasmobranchii*.

The polar cartilage of these fishes thus apparently being the pharyngeal element of the mandibular arch, its relations to the trabecula strongly suggest that that cartilage is the corresponding element of the premandibular arch. The dorsal end of the skeletal bar of the latter arch must have lain, primarily, directly ventral to the acrochordalis tissue, and it should there normally have acquired contact or connection with the axial skeleton. This has, however, been prevented partly by the failure of the acrochordalis tissue to chondrify, but mainly because of changes in the region associated with the development of the mouth and the hypophysis. Some fixed support was, however, needed, because of the supporting relations of the cartilage to the roof of the mouth, and it was acquired by fusion with the distal end of the polar cartilage, fusions of the cartilages of one arch with those of an adjoining one being of frequent occurrence in fishes. Furthermore, this assumption offers an explanation of the otherwise apparently inexplicable course of the efferent mandibular artery of these fishes dorsal, instead of ventral to the trabecula.

In *Acanthias*, as above stated, the polar cartilage fuses with its fellow of the opposite side both dorsal and ventral to the lateral dorsal aorta (internal carotid), as well as fusing with the ventral surface of the parachordal dorsal to the latter vessel. What has been the cause of this fusion with its fellow of the opposite side is not apparent, but, as a result, the lateral dorsal aortae are forced together in the median line and there fuse with each other, the point



of fusion lying between the points where the aortae are joined by the efferent arteries of the hyal and mandibular arches. The fusion of these arteries completes the well-known circulus cephalicus, and the efferent mandibular artery of either side is pulled slightly postero-mesially, and hence, in its course upward and inward to reach and fall into the aorta, it crosses the anterior edge of the pharyngomandibular (polar cartilage) definitely dorsal to its ventral end. The efferent artery accordingly lay dorso-posterior to the point of contact of the pharyngomandibular with the pharyngopremandibular when these two elements fused with each other, and hence lies, actually, dorsal to the latter element, this being the reverse of its normal relations. The lateral dorsal aorta lies, on the contrary, actually mesial, but morphologically ventral, to the pharyngopremandibular, and this relation to that cartilage would necessarily result from the fusion of the cartilage with the pharyngomandibular whether the pharyngopremandibular were, before the fusion, directed towards the cranium ventral or dorsal to the aorta, provided only that, in the latter case, the arteria cerebralis ran upwards anterior to the pharyngopremandibular. If the artery ran upwards posterior to the pharyngopremandibular (which seems improbable), and the latter element had acquired contact or connection with the cranium dorsal to the aorta, it might, in fusing with the pharyngomandibular, have pushed the base of the arteria cerebralis outwards, thus forcing it to run upwards lateral and then dorsal to the pharyngopremandibular, as it actually does both in the adult *Polypterus* and in the youngest larvae of that fish that have as yet been examined and described.

In *Scyllium* the conditions differ from those in *Acanthias* in that the pressure, or pull, tending to force the pharyngeal elements of the mandibular and premandibular arches into a position parallel to the axis of the body, has caused a bending upwards and backwards of the anterior end of the notochord, instead of a bending upward and forward of the trabeculo-polar bar; and in both these fishes the impulse did not become effective, so far as the pharyngomandibular is concerned, until after that element had become firmly fused with the parachordal.

If the polar cartilage is the pharyngomandibular, the palatoquadrate must be the epimandibular. The processus basalis and processus palatobasalis are then, respectively, the posterior and anterior corners of the greatly expanded dorsal (proximal) end of this element of the arch, and the processus muscularis (metapterygoideus) is part of a ridge which, as in the branchial arches, formed, primarily, the anterior edge of a groove on the external edge of the element to lodge the arteries and nerves of the arch.

In the *Holostei* and *Teleostei* the conditions differ from those above described in certain important details, but not in principle.

In a 10 mm. embryo of *Lepidosteus*, Veit (1911) shows the trabecular and polar cartilages of either side lying one anterior to the other in the horizontal plane of the related parachordal. In 11 to 12 mm. embryos these primarily independent cartilages have fused with each other and with the parachordal,



and the efferent mandibular artery joins the internal carotid ventral to, instead of dorsal to, the so-formed trabeculo-polar bar (Allis, 1909, p. 186). After receiving this artery, the carotid turns upwards between the hind ends of the trabeculae and not, as in the Elasmobranchii, between the polar cartilages.

In an embryo of *Amia* 8 to 8.8 mm. in length, Pehrson (1922) finds the polar cartilage of either side already fused with both the parachordal and trabecula, but still readily recognizable. It is said to be triangular in shape, the base of the triangle directed forwards, and it is with the lateral one of the two corners of the base that the trabecula has fused. The mesial corner projects slightly forward, and the internal carotid runs upward in the space between this projecting corner and the trabecula. In later stages the projecting mesial corner also fuses with the trabecula, thus enclosing the carotid in a foramen, and this foramen evidently becomes the carotid canal of the adult, which traverses the presphenoid bolster (Allis, 1897). The dorsal end of the efferent mandibular artery, which primarily joined the internal carotid ventral to the trabecula (Allis, 1919, p. 266), also becomes enclosed in the cartilage, and hence, in the adult, has the appearance of traversing the trabecula.

The efferent mandibular (pseudobranchial) artery thus has, in these two ganoids, distinctly different relations to the trabecula from those that it has in the Elasmobranchii, but this is evidently due to the fact that the internal carotid (lateral dorsal aorta) has not here been crowded inwards to the median line by the fusion of the pharyngomandibulars (polar cartilages) of opposite sides, and that the latter cartilages have not fused with the axial skeleton until after they and the pharyngopremandibulars (trabeculae) have both acquired a position in the horizontal plane of the parachordals. Because of this, the ventral end of the pharyngomandibular, in swinging upward, has passed postero-dorsal to the efferent artery of its arch, that artery being held in position distal to the pharyngeal element, between the two process-like corners of the expanded dorsal end of the epimandibular, by its attachment to the carotid. The carotid (lateral dorsal aorta) of either side accordingly runs forwards ventral and mesial to the trabeculo-polar bar until it has received the efferent mandibular artery, when it turns upwards along the actually mesial but morphologically anterior edge of the hind end of the trabecula and enters the cranial cavity, this point corresponding to the point where, in the Selachii (and hence probably in others also of the Elasmobranchii), the artery, after receiving the efferent mandibular artery, pierces the lining membrane of the cranial cartilage and enters the central cavity. The ventral edges of the polar cartilages later grow towards each other, dorsal to the internal carotids, and certainly form the anterior portions of the lateral bounding walls of the pituitary fossa, but whether it is outgrowths of these cartilages, or of the parachordals, that form the posterior portions of those walls cannot be told from the descriptions and figures. It would however seem quite certain that the posterior portions of the walls are of parachordal origin, and correspond to the ventral processes of the median basisphenoid of Stensiö's (1921) de-

scriptions of *Wimania* and *Axelia*. But however this may be, the internal carotid of either side lies along the external surface of the wall.

In embryos of the non-silurid Teleostei the conditions are probably similar to those in the Holostei, for Stöhr (1882) describes, in early embryos of *Salmo salar*, an independent cartilage which must be a polar cartilage, lying between the trabecula and parachordal. This cartilage is said by him to fuse first with the parachordal and then with the trabecula, and it is evidently represented, in the descriptions of these fishes by other authors, in the so-called anterior prolongation of the parachordal. In an 11 mm. embryo of *Salmo trutta*, Dohrn (1886) shows these three cartilages already fused to form a continuous bar, and the internal carotid artery runs forward beneath that part of this bar apparently formed by the polar cartilage, there receives the efferent mandibular (pseudobranchial) artery, and then turns upwards through the space enclosed between the trabecular portions of the bars of opposite sides. Up to this point, the carotid is not at any point connected with its fellow of the opposite side either by anastomosis or commissure, the conditions in these embryos thus being similar to those in the Holostei.

In the adults of all of the non-silurid Teleostei that I have examined, the conditions are markedly different from those above described in trout embryos, for, in later stages of development of all these fishes a certain portion of the trabeculo-parachordal bar undergoes resorption, this resorption apparently involving either the polar cartilages alone, or portions of the adjoining ends of those cartilages and the trabeculae. Associated with this, and with the development of a ventral myodome compartment, the internal carotids are pressed together in the median line there to fuse with each other as they run upwards in the median vertical myodome membrane, and the efferent mandibular arteries lose their primitive connections with the internal carotids and become connected with each other by cross-commissure. These connections of these arteries are shown by Dohrn (1886) in an 18 mm. embryo of *Salmo trutta*, the anastomosis of the internal carotids lying anterior to the hypophysis, and apparently anterior also to the point where the carotids were primarily joined by the efferent mandibular arteries. The anastomosis between the carotids of these fishes is thus quite certainly not the homologue of the anastomosis in the Plagiostomi. The further course of the internal carotid is not given in advanced stages of *Salmo*, but in such stages of several others of the non-silurid Teleostei that I have examined (Allis, 1919), the internal carotid, distal to its anastomosis with its fellow of the opposite side, separates into anterior and posterior divisions, and the anterior division runs forwards in the dense fibrous tissue which forms both the dorsal edge of the interorbital septum and the floor of the corresponding part of the cranial cavity, and only enters the latter cavity after it reaches the region of the optic chiasma, that being the region in which the main artery enters the cranial cavity both in the Plagiostomi and the Holostei.

In the Siluridae somewhat different conditions exist. In a 10 mm. embryo



of *Amiurus*, Kindred (1919) shows the trabecula and parachordal of his descriptions already fused to form a single continuous piece, and a polar cartilage must be included in it. The internal carotid runs upwards through a notch in the mesial edge of this continuous bar, this notch being said to lie in or about the middle region of the orbit, and hence certainly anterior to that part of the trabeculo-parachordal bar that corresponds to the polar cartilage. In a 32 mm. larva the condition of these arteries is apparently similar to that which I have described in the adult (Allis, 1908 b), for Kindred says (*l.c.* p. 35): "In the younger stage the internal carotid artery enters the cranium internal to the trabecula, but now it has a different relation. This blood vessel enters a rete mirabile, lateral and posterior to the optic foramen, and a branch to the internal part of the cranium enters through the posterior part of the optic foramen. The external carotid enters the cranium as before, between the branches of the trigeminal nerve."

The conditions in embryos of *Amiurus* between the two stages above referred to, are not given by Kindred, but it is evident that, during this interval, the internal carotid has cut through the trabeculo-parachordal bar in the region of the fusion of the trabecula with the polar cartilage. How this has taken place is not indicated, but it is said (*l.c.* p. 37) that the trabeculae of the 32 mm. larva "are no longer continuous bars from the ethmoid plate to the parachordal plate, but half-way between those regions a part of each has been resorbed and parasphenoid and suprasphenoid ossifications have replaced it by growth dorsally into this region, forming the posterior margin of the optic foramen and part of the margin of the trigemino-facial foramen."

During this process of resorption of the cartilage, and its replacement by bone, the internal carotid must have slipped outwards to the external surface of the cranium, the artery thus cutting through the cartilage in a manner strictly comparable to that described by Gaupp (1893, p. 403) for the corresponding artery in *Rana*. The same result would evidently have been attained if, in a fish where the conditions were as in the 8 mm. embryo of *Amia* described by Pehrson, the secondary fusion of the trabecula with the mesial corner of the polar cartilage were to persist, and the primary fusion, with the lateral corner of that cartilage, be resorbed. The point where the artery of *Amiurus* finally enters the cranial cavity is, it is to be noted, approximately the same as in the other fishes above referred to. That the external carotid of this fish should enter the cranium with the branches of the nervus trigeminus, as stated by Kindred, seems unusual.

In a 75 mm. specimen of *Polypterus*, I found the carotid artery running forwards along the external surface of the cranium until it reached the optic foramen, and there entering the cranial cavity immediately posterior to the optic nerve (Allis, 1908 a); and Budgett (1902) shows the artery in a similar position in a 30 mm. embryo of this fish. The artery in this case passes dorsal to the trabecula to enter the cranial cavity, as it does in advanced stages of *Amiurus*, but there is nothing in the two stages of *Polypterus* to indicate that



the artery has cut through the trabeculo-parachordal bar, as it has in *Amiurus*. Earlier stages in the development of this fish must be known before this course of the artery can be properly accounted for.

In an embryo of *Ceratodus* of stage 48, Greil (1913) shows the internal carotid, after receiving the efferent mandibular artery, crossing the ventral surface of a part of the trabeculo-parachordal cartilage that corresponds strictly in position to the polar cartilage of the fishes above referred to. The artery then turns upwards along the mesial edge of the trabecular part of the bar and is connected with its fellow of the opposite side by a cross-commissural vessel which lies posterior to the hypophysis and apparently dorsal to the anterior end of the parachordal plate, the conditions thus being strictly similar to those in the 11 mm. embryo of *Salmo trutta* described by Dohrn excepting in the position of the cross-commissural vessel between the carotids of opposite sides.

In higher vertebrates, the polar cartilages have been described in certain Aves and Mammalia. In the chick and duck the conditions, as described by Sonies (1907), are strictly comparable to those in certain fishes, excepting in the presence of a so-called *processus infrapolaris* which projects posteriorly from the dorsal end of each polar cartilage, ventral to the internal carotid (lateral dorsal aorta), and in certain Aves fuses, posterior to that artery, with the parachordal plate. This process and the dorsal end of the polar cartilage of these vertebrates thus have to the internal carotid (lateral dorsal aorta) exactly the same relations which the two fusions of the polar cartilage of *Acanthias*, with its fellow of the opposite side, have to the same artery, the only difference being that in the one case processes of the polar cartilages fuse with the parachordal, while in the other they fuse with their fellows of the opposite side; and this is evidently related to the absence of a *circulus cephalicus* in the one and its presence in the other. The ventral of these two fusions represents the primitive relation of the cartilage to the internal carotid (lateral dorsal aorta), and if it alone were to persist, the artery would pass lateral and then dorsal to, instead of ventral and then mesial to the trabecula, as already suggested in one of my earlier works (Allis, 1919).

In *Talpa*, as described by Noordenbos (1905), there is, in early stages of development, a Y-shaped cartilage between the polar cartilages and the parachordal plate, this cartilage representing that fusion of the polar cartilages of *Acanthias* lying dorsal to the internal carotids.

The relations of the internal carotid and efferent mandibular arteries of the gnathostome vertebrates to the polar and trabecular cartilages thus strongly suggest that those cartilages are, respectively, the pharyngeal elements of the mandibular and premandibular arches, and if this be so it would seem to follow that the epal element of the premandibular arch, or at least its proximal portion, is represented in the palatine process of the palatoquadrates, that is, in that part of the latter cartilage that lies anterior to its orbital (palato-basal) process. The antorbital wall would then probably have been

developed from tissues that are serially homologous with those that give origin to the hyomandibula in the hyal arch of the Teleostomi, and, in the mandibular arch, to the lateral wall of the trigemino-facialis chamber; and the fact that the dorsal end of the antorbital wall fuses with the dorsal end of the dorso-anteriorly directed alisphenoid cartilage, derived from the pre-mandibular somite, is suggestive of such an origin. The prechordal portion of the chondrocranium, exclusive of the sense-organ capsules, would then be wholly of visceral-arch origin, and the enclosure within it of any portion of the brain would be a secondary adaptation.

The chiasma-ridge is generally considered to mark the anterior end of the floor of the brain of the adult vertebrate, but Kingsbury (1920) contends that this ridge simply marks the anterior end of the embryonic neural plate, the actual floor-plate of the brain ending, considerably posterior to it, at the fovea isthmi, which lies, in the adult, slightly posterior to the central point of the summit of the plica encephali ventralis. The floor-plate of the brain and the notochordal plate are said by him to have been primarily coextensive.

All that part of the ventral surface of the adult brain that lies between the fovea isthmi and the chiasma-ridge must therefore have formed, primarily, some part of the anterior surface of the brain, and quite probably the whole of it, and the conditions in recent vertebrates show conclusively that this anterior surface of the brain swung downward and forward over the tip of the notochord until it came in contact with the pharyngopremandibulars (trabeculae). This gave rise to the plica encephali ventralis, and when the pharyngopremandibulars later swung upward into the plane of the parachordals, the brain was bent upward and backward and so gave rise to the marked curvature (*Brückenbeuge*) found in many vertebrates at the base of the posterior limb of the plica.

The anterior surfaces of the brain and pharyngopremandibulars were certainly, at this early period, covered externally by a layer of ectoderm but slightly separated from them. The middle point of the transverse line separating these two ectodermal surfaces lay in close proximity to the infundibular region of the brain and to the dorsal surface of the anterior end of the archenteric cavity, and it must have already acquired relations to the infundibular tissues, thus forming the beginnings of the hypophysis. As the anterior surface of the brain then swung downward and forward to acquire contact with the pharyngopremandibulars, the related cerebral and visceral-arch ectodermal surfaces must either have been pushed bodily away from the underlying structures, or have been folded, hinge-like, one upon the other, and in either case the hypophyseal tissue would have been held in place by its acquired relations to the infundibulum and hence have given rise either to a short hypophyseal pit, or to a solid cord of ectodermal tissue. That the hypophyseal pit or cord could have been developed after the chiasma-ridge had acquired contact with the pharyngopremandibulars, seems wholly improbable, for in that case an undifferentiated portion of the ectoderm would have had to start out from a



relatively distant point—in *Amia* close to the neuropore (Reighard and Mast, 1908)—either by invagination or solid ingrowth, to seek and find certain nervous tissues with which it had to become associated in order to establish its own special and particular function.

The hypophyseal pit would have lain, at this period, wholly antero-dorsal to the pharyngopremandibulars (trabeculae), with its external opening in the region of the chiasma-ridge, and there lying between ectodermal surfaces that cover, the one that part of the external surface of the brain that lies between the chiasma-ridge and the neuropore, and the other that part of the external surface of the anterior end of the branchial chamber that lies ventral to the outer ends of the pharyngeal elements. The snout had not as yet been developed; and, as the nasal epithelium develops in relation to it, and it encloses the anterior portions of the trabeculae, it is evident that it contains tissues derived both from the cerebral surface just above referred to—which may be called the frontal surface—and from the visceral-arch surface. The dorsal edge of the latter surface lies postero-ventral to the opening of the hypophyseal pit. In order that the pharyngopremandibulars and the tissues related to them could take part in the formation of the snout, they would accordingly have to grow forward either ventral or lateral to the pit. In the former case the pit would be gradually deepened by the progressive coalescence of its edges, and might readily be prolonged until its external opening reached the ventral edge of the neuropore, this giving rise to the conditions actually found in the Cyclostomata and Ganoidei; and that the pit was here quite certainly formed by the gradual coalescence of its edges, and not by invagination, would seem to be shown by its development in *Petromyzon*, for the slight indentation in the ectoderm that there marks its first appearance lies in the region of the optic recess, and not near the neuropore (von Kupffer, 1894). When the visceral-arch tissues passed lateral to the hypophyseal pit, they would have fused again immediately beyond it, the opening of the pit then lying ventral to the plane of the trabeculae, and ultimately in the stomodaeum, as it does, so far as I can find described, in all vertebrates excepting only the Cyclostomata and Ganoidei.

When, under this assumption, the pharyngopremandibulars grew forward lateral to the hypophyseal pit, they would either be carried, by this growth, bodily forward beyond the pit, or be pushed there by a correlated growth of the pharyngomandibulars (polar cartilages), the pharyngopremandibulars then fusing with each other beyond the pit and so forming the anterior wall of the pituitary fossa; and, whether they passed lateral or ventral to the pit, they would drag after them the epipremandibulars (palatine processes). The epimandibulars (palatoquadrates) would undergo a correlated anterior prolongation and fuse with the distal (hind) ends of the epipremandibulars to form the palato-pterygoquadrates, this giving rise to the well-known maxillary processes of vertebrate embryos. Whenever, in this process, the palato-pterygoquadrates did not retain fixed articular relations with the pharyngopre-



mandibulars (trabeculae), the maxillary processes of opposite sides would meet and fuse in the median line anterior to the hypophyseal pit, and so form the entire primary upper edge of the mouth, as occurs in the embryos of certain vertebrates; but whenever this articular relation was retained, the maxillary processes would not so meet in the median line, fusing, instead, with either the frontal or nasal processes, derived from the frontal ectodermal surface. In the latter case, the median portion of the upper edge of the mouth would nevertheless quite certainly be formed by tissues related to the epipremandibulars, for that part of the palato-ptyergoquadrate of the Teleostomi that corresponds to the palatine processes of the Selachii lies anterior to the ridge that forms the hind edge of the surface of articulation with the ectethmoidal (antorbital) process, and a certain median portion of it, which primarily formed the median portion of the upper edge of the mouth, was quite certainly later detached and finally resorbed (Allis, 1914). The frontal and nasal processes are derived from the frontal ectodermal surface and take no part in the formation of the primary upper edge of the mouth.

In the Ganoidei there is an adhesive organ on the anterior end of the snout, formed of two organs, one on either side. The fundament of this organ first appears, in *Amia* (Rieghard and Phelps, 1908), as a crescent-shaped and elevated area which lies directly in front of the optic vesicles and forebrain, and directly external to a dorsally directed diverticulum of the archenteric cavity. The crescent-shaped area later separates into three hemispherical protuberances, a median one called the button, and two lateral ones which form the fundaments of the two adhesive organs. The hypophysis lies between the button and the anterior surface of the brain, and the stomodaeum anterior to the button and the two lateral protuberances. From the dorsal wall of the short foregut three diverticula arise, the median one related to the button and the lateral ones to the two adhesive organs. The button later disappears by a process of transformation into mesoblast, but the diverticula related to the adhesive organs ultimately break through to the external surface: and Reighard and Phelps express their belief that these diverticula are homologous with the so-called anterior head cavities of selachian embryos.

In *Acipenser*, a part of the fundament of the adhesive organs is shown by von Kupffer (1893) lying in the median line antero-ventral to the hypophysis, the primitive conditions in this fish thus apparently being similar to those in *Amia*. In embryos of *Polypterus*, two adhesive organs are shown by Kerr (1903), but they lie one on either side of the stomodaeum, instead of on the anterior end of the snout, and nothing is said as to their having been primarily connected by a median button. Kerr however says that in occasional embryos the two organs are found fused with each other in the median line, but it is not said on which side of the hypophysis the organs then lie. When the organs are not fused the hypophysis lies between them, in the stomodaeum.

It thus seems probable that it is the fusion, in the median line, of the fundaments of the adhesive organs of opposite sides that causes the displace-

ment of the hypophysis in the Ganoidei, and this is exactly what might be expected under the theory here proposed, for, as the hypophysis lies between the fundament of the organ and the anterior end of the brain, the fundament must have been developed in what I have called the visceral-arch tissues, and if the central point of the fundament, the button of Reighard and Phelps' descriptions of *Amia*, persisted until after the snout had begun to be developed, the visceral-arch tissues could not readily have separated in the median line in order to pass on either side of the hypophyseal pit, while if the button had been dispersed at an earlier stage they could have so separated.

In *Petromyzon* no adhesive organs have been described, so far as I know, but the upper lip of this fish has been compared to that part of the snout of the Ganoidei that bears these organs, and the external opening of the hypophysis lies close to the neuropore.

The arteria cerebralis was probably sent upward, primarily, along the anterior edge of the premandibular somite, and it is apparently a serial homologue of the cerebral branches of the intervertebral arteries related to more posterior somites, but as that part of the brain to which it is related projects forward beyond the anterior opening of the chordal portion of the cranium, the artery has followed it, and accordingly, in all the fishes above considered, first enters the central cerebral cavity in the region of the optic chiasma.

If the epipremandibulars are the palatine processes of the palatoquadrates, as here suggested, the dorsal portions, at least, of the mandibular clefts could not have been utilized to form part of the buccal opening, and if these portions of the clefts persisted as evaginations of the foregut, they would probably be represented in the diverticula related to the adhesive organs.

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## THE BLASTOCYST OF THE DOG

By O. VAN DER STRICHT.

IN a previous paper<sup>1</sup>, based on my own investigations and those of my pupils, I have emphasised the importance of studying the structure of the ova of mammals during all stages of ovogenesis. The morphology of the yolk is characteristic for each species and does not undergo any fundamental change by fertilisation. Hence the hereditary substratum, involving the morphological characters of a species, depends exclusively, in my opinion, on the female sexual cell.

With regard to the dog, the characteristic structure of the yolk is due to the peculiar arrangement of chondriomites and chiefly to the extraordinary abundance of fat granules. On the present occasion, I wish to demonstrate how long this structure persists in the young embryo and at the same time to describe briefly four successive phases of development of the blastocyst.

During the first two stages, the cytoplasm of the embryonal cells remains laden with fat granules; in the trophoblastic elements, the lipid granules persist only in the endoplasm of the cells and disappear in the broad zone of exoplasm. During the last two stages, the granules gradually diminish in number and diameter, namely towards the internal pole of the embryonal ectoblastic cells and also in the trophoblastic elements.

This morphology, as is shewn in my photographs, is clearly visible not only during ovogenesis and segmentation but also in the blastocysts. Photographs of the external surface of the entire blastodermic vesicle shew a layer of flattened cells, made up of a clear nucleus, a perinuclear endoplasm zone, dotted with fat granules and a large clear zone of exoplasm, destitute of lipid globules. At first sight there seem to exist broad intercellular spaces. This picture of the trophoblastic wall resembles that given by J. P. Hill for *Dasyurus* (figs. 27-30, Pl. 3, *Quart. Journ. Micros. Sci.* vol. 56). A solution of nitrate of silver however renders evident, in black, the lines of intercellular cement and demonstrates that no real but only very small and few gaps are present.

In photographs of stained sections across the embryonal region of the blastocysts are visible the unilaminar trophoblastic layer and the inner cell-mass. In the first stage of development, this latter is a convex knot, attached to the inner surface of the trophoblast and projecting into the fluid of the blastodermic cavity. As the result of the increasing high pressure of this liquid, the knot gradually becomes flattened out.

<sup>1</sup> O. van der Stricht: "Étude comparée des œufs des Mammifères," *C. R. de l'Assoc. des Anatomistes*, 17<sup>e</sup> Réunion (Gand, 1922).

At this early stage of development, the blastocyst is unilaminar in its extra-embryonal region and didermic in its formative region. At a second and later stage it becomes monodermic also in the latter region. Indeed by pressure, the knot compresses and gradually repels laterally, outside the embryonal pole, the overlying cells of Rauber's layer. Eventually the knot is intercalated within the unilaminar layer of the blastocyst which is now everywhere monodermic. This stage recalls that of Marsupials (J. P. Hill).

A third following phase is characterised by the appearance of virtual hypoblastic elements. As the embryonal layer or knot flattens out, it becomes thinner and a few small cells seem to be forced or compressed towards its inner surface, next the blastocyst cavity; these give rise to the lecithophore or hypoblast which is now virtually laid down. Some of these cells extend on to the inner surface of the neighbouring trophoblast. But if the internal pressure ceases, as happens when the wall of the blastocyst is torn before preservation, the didermic embryonal mass becomes monodermic again, because the delamination of the lecithophore was not yet completed.

At a fourth stage, the hypoblastic elements are absolutely independent and separated from the ectoblast. They form a layer of flattened cells which sooner or later become columnar in the future cephalic half of the embryonal area. In this way, the latter acquires its bilateral symmetry. At the same time, hypoblastic elements continue to extend on the inner surface of the trophoblast. The blastocyst becomes didermic everywhere.

No definite statements can be given as to the precise diameter of the various stages of development. I am only able to state that generally blastodermic vesicles of the first stage vary in diameter from 0.20 to 0.30 mm., those of the second stage, from 0.30 to 0.40 mm., those of the third stage from 0.70 to 0.80 mm., and those of the fourth stage from 1 to 1.5 mm. There is much variation, dependent probably on the size of the dog, on the occurrence of more or less advanced phases in the same mother, and even on injuries suffered by the living blastocyst prior to preservation.

# THE LOBE OF THE AZYGOS VEIN

## NOTE ON TWO ADDITIONAL CASES

BY JOHN CAIRNEY, M.B., CH.B. (N.Z.),

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DURING the past few years there have been observed in the dissecting-room of this department two cases of abnormal lobation of the right lung; one case occurred in November, 1918, and the other in November, 1921. In each instance the anomaly consisted in what has been variously termed by different writers the lobe of Wrisberg, the azygos lobe, and the lobe of the azygos vein, i.e. a lobe cut off from the upper and medial part of the lung, above the hilus, by a fold of parietal pleura containing the vena azygos major. Fig. 1 represents a photograph of a cast of the lung of the second case; the vena azygos major is shown occupying the base of the fissure which separates the lobe of the azygos vein from the rest of the lung.

This type of anomaly has been described by a number of writers since Wrisberg, who described the first recorded case in 1778. In 1919, E. Philip Stibbe, writing in the *Journal of Anatomy*, described a case which he had observed, and collected 22 other cases from the literature. I follow Stibbe in using the term "lobe of the azygos vein," which was also used by D  v  .

Although the anomaly appears to be rare, accurate descriptions have been given by most of the previous writers to whose papers I have access, and the general features are apparently sufficiently well recognised to render further complete descriptions unnecessary. The condition is described by Charpy in his account of the venous system in Poirier and Charpy's *Traite d'anatomie humaine*, under the heading of "Passage de l'azygos dans une scissure pulmonaire."

### PARTICULARS OF CASES

Stibbe, in his paper already referred to, tabulated all the cases which he had collected under a series of headings which showed the points of resemblance and of difference. I therefore present, under practically the same headings, the particulars of the two further cases which I have seen.

#### *Case I*

1. Subject: Male aged 84.
2. Position of fissure: Vertical, cutting the apex of the lung.
3. Depth of fissure: Practically to the hilus.
4. Level at which vena azygos major deviates to the right before entering the fissure: Not recorded.
5. Termination of vena azygos major: Normal.



6. Remarks: The lobe measured approximately, from above down 3 inches, from before back  $1\frac{1}{2}$  inches, from within out  $1\frac{1}{4}$  inches. Its apex was at the level of the 7th cervical vertebra, and at the same level as the apex of the rest of the lung.



Fig. 1. Cast of the right lung of Case II, as seen from the medial side. The cut end of the vena azygos major is seen in the fissure between the lobe of the azygos vein and the rest of the upper lobe.

Fig. 2. Cast of the eparterial bronchus and its branches in Case II, as seen from the medial side, showing the primary division into horizontal and vertical branches. Of the vertical branches, *A* and *B* are the two branches directed towards the main apex of the lung, and *C* is the branch which enters the lobe of the azygos vein. The vena azygos major is shown lying transversely between branch *C* on its medial side and branches *A* and *B* on its lateral side.

Fig. 3. Cast of the right lung of a porpoise, as seen from the medial side. The vena azygos major is shown occupying the fissure between the lobe of the azygos vein and the rest of the upper part of the lung.

### *Case II*

1. Subject: Adult male.
2. Position of fissure: Vertical, cutting the apex of the lung.
3. Depth of fissure: To about midway between the apex of the lung and the hilus.
4. Level at which vena azygos major deviates to the right before entering the fissure: 5th thoracic vertebra.
5. Termination of vena azygos major: Ends by joining the lateral aspect of the right innominate vein at the level of its junction with the left innominate vein.

## 6. Remarks:

(i) The lobe measures approximately, from above down  $1\frac{3}{4}$  inches, from before back  $1\frac{1}{4}$  inches, from within out  $\frac{1}{2}$  to  $\frac{3}{4}$  inch.

(ii) The right internal mammary vein joins the ventral aspect of the right innominate vein at the same level as the vena azygos major joins its lateral aspect.

I also append, as far as possible, similar particulars of a case recorded by Fischer in 1899, but not included in the table given by Stibbe.

1. Subject: Male aged 58.

2. Position of fissure: Not definitely stated. It is, however, stated, in different parts of Fischer's paper, that the lobe was directed inwards as well as upwards; that the lobe was given off from the medial aspect of the main upper lobe; and that the apex of the lobe was situated one vertebra lower than the apex of the main upper lobe. From these statements it is assumed that the fissure cut the medial surface of the lung below the apex.

3. Depth of fissure: About 5 cm., its base being at the level of the 4th thoracic vertebra.

4. Level at which vena azygos major deviates to the right before entering the fissure: 4th thoracic vertebra.

5. Termination of vena azygos major: Figured as opening into superior vena cava just below the union of the two innominate veins.

## 6. Remarks:

(i) The lobe measured, from above down 5 cm., from before back 4 cm., from within out 2 cm.

(ii) The middle lobe of the lung was unusually small, and less sharply marked off from the upper lobe than usual.

## POSITION OF THE FISSURE

In the course of a discussion on the features of all the cases collected by him, Stibbe pointed out that, as regards the position of the fissure separating the lobe of the azygos vein from the rest of the lung, the cases might be divided into three types, viz. type *a*, in which the fissure cuts the lateral surface of the lung below the apex; type *b*, in which the fissure is practically vertical and cuts the apex; type *c*, in which the fissure cuts the medial surface below the apex. Stibbe further showed that, in 19 cases in which the position of the fissure was mentioned, type *a* occurred in 9 cases, type *b* in 5, and type *c* in 5.

The two cases which I have seen are both of type *b*, and Fischer's case appears to have been of type *c*. The addition of these three cases to those mentioned by Stibbe gives, for a total of 22 cases, 9 cases of type *a*, 7 cases of type *b*, and 6 cases of type *c*. To a slight extent this bears out the suggestion made by Stibbe that probably a larger number of cases will show more nearly equal numbers in each of the three groups.

## THE BRANCHING OF THE EPARTERIAL BRONCHUS IN ONE CASE

In the second case observed in this department, the eparterial bronchus and its branches were dissected out as far as possible. A cast of this bronchus and its branches is represented in fig. 2. Briefly, the arrangement found was as follows.

The eparterial bronchus, after a very short course, divides into three branches, two in the horizontal plane and one ascending vertically.

Of the two branches in the horizontal plane, the anterior almost immediately divides again into two. Thus are produced in all three branches in the horizontal plane. Of these the anterior one is directed ventrally, while the other two are directed laterally. The two branches directed laterally are not evident in the figure.

The vertical branch, on being traced upwards, divides into:

(a) A branch directed upwards, forwards, and outwards towards the main apex of the lung (marked *A* in the figure).

(b) A branch continuing a vertical course definitely medial to the other. It gives off a smaller branch (*B* in the figure) directed upwards, backwards, and outwards towards the main apex, and then itself (*C* in the figure) enters the lobe of the azygos vein. It presents a slight curve, the concavity of which corresponds to the position of the vena azygos major at the base of the fissure.

Thus the first vertical branch of the eparterial bronchus gives place, after a certain distance, to three branches; of these, one (marked *C*), directed upwards medial to the other two, supplies the lobe of the azygos vein, while the other two (*A* and *B*) pass towards the main lung apex. This practically corresponds to the condition found by Geddes and others, who state that, in their cases, the eparterial bronchus gave off three branches directed towards the apex of the lung, of which the medial one supplied the lobe of the azygos vein. It differs, however, from the arrangement described by Matthews, in whose case two distinct branches entered the lobe of the azygos vein.

THE OCCURRENCE OF THE LOBE OF THE AZYGOS  
VEIN IN THE PORPOISE

Certain of the previous writers on the subject have mentioned the presence of the lobe of the azygos vein in the porpoise. Allen in 1882 mentioned having seen the condition in a porpoise, but regarded it as "problematical whether this state of matters is the rule or the exception." Matthews in 1898 wrote as follows: "Allen reports finding a portion of the upper lobe of the right lung in a porpoise, constricted by the vena azygos major, but there does not appear to be any other recorded case of a similar condition in animals." Geddes in 1910 expressed the opinion that the condition was "frequent if not constant in the porpoise." while Holtby in 1915 stated that he had been informed by Waterston that the condition is constant in the porpoise.



In a porpoise dissected here recently, a lobe of the azygos vein was definitely present in the right lung, while the left lung showed no corresponding lobe. Fig. 3 represents a cast of the right lung in this particular case.

#### SUMMARY

1. Stibbe in 1919 collected 23 cases of the anomaly known as the lobe of the azygos vein, and tabulated the various points of resemblance and of difference. Three further cases are here presented, two of which represent personal observations, while the third is a case described by Fischer in 1899, but not included in Stibbe's series. The particulars of these cases are shown under headings similar to those proposed by Stibbe.

2. The position of the fissure with regard to the apex of the lung is briefly discussed. Of the 26 cases of which particulars are now available, the position of the fissure appears to be determined in 22. Of these, the fissure cuts the lateral surface of the lung below the apex in 9 cases, is practically vertical and cuts the apex in 7, and cuts the medial surface below the apex in 6.

3. The branching of the eparterial bronchus in one case is described, the general arrangement corresponding to that found by certain previous writers upon this subject.

4. Reference is made to the occurrence of the lobe of the azygos vein in the right lung of the porpoise, and a cast of such a lung is figured.

In conclusion I wish to record my thanks to Dr W. P. Gowland, Professor of Anatomy in the University of Otago, for permission to publish the two cases which have occurred here, as well as for many valuable suggestions in the preparation of this paper.

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# ON THE MUSCULAR ARCHITECTURE OF THE VERTEBRATE VENTRICLE

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USING a new method of dissection, J. B. MacCallum (1900) solved the old and baffling problem of the arrangement of the muscle fibres in the mammalian ventricle. After MacCallum's untimely death, Mall (1911) applied the same method to the human heart. Although Mall's paper is difficult to follow, his skilfully chosen and wonderfully executed drawings afford the best of dissection directions; and with their help, we can now understand a structure that has perplexed anatomists from Vesalius onwards.

The attention of anatomists has hitherto been directed almost entirely to the mammalian heart. Pettigrew (1864) is almost the only one who has attempted to unravel the hearts of other vertebrates. It seemed to me, therefore, worth while to re-examine with modern methods the hearts of other forms; to see what resemblances or differences there are between the mammalian and bird heart, where the mechanical requirements are so similar; and to find out the relation of both to the hearts of the fish, frog, and reptile.

I shall describe first the ventricle of the common fowl, pointing out its relations to the mammalian heart, and then take up each of the other forms in turn.

## VENTRICLE OF THE FOWL

A detailed description of the gross anatomy of the bird heart can be found in various texts; that of Owen (1866) is very good. For the present study, the following peculiarities should be kept in mind. The small chordae tendineae, which are attached to the two leaflets of the right atrio-ventricular valve, either sink at once into the muscular wall of the ventricle, or have very short papillary muscles. The right atrio-ventricular orifice is guarded by a large fleshy, lateral valve, which is quite different from the one found in mammals (fig. 5). No chordae tendineae are attached to it; the inner wall of the right ventricle is notably smooth. The right ventricle does not extend to the tip of the heart, and the apex is formed by the left ventricle alone.

To make as clear as possible a most difficult subject, I will first describe the steps in the dissection of a single heart, after the manner of a dissecting manual, and then summarise with a formal description of the separate muscles.

Hearts of the common fowl were preserved in 10 per cent. carbolic acid. To prepare for dissection, the hearts were soaked overnight in dilute acetic acid, and then allowed to simmer for fifteen minutes. The gentle heat toughens the muscle and softens the connective tissue. Boiling contracts the hearts too much.

Take a heart, prepared as above directed, and clean off the fat and pericardium under a dissecting microscope. The pericardium is tough, and the superficial heart muscle easily comes away with it. Snip off the aorta and pulmonary artery, and snip off or pull out the atria. The latter come off easily, for the atrio-ventricular connection is formed chiefly of connective tissue. Pick away from the apex the lump of fat invariably found there, and bring out the details of the vortex by judicious kneading, or with a dull probe.

The base of the heart then appears as in fig. 1. From the four great orifices, whose general relations to each other are little different from the mammal, spring the superficial muscle fibres. In general, the fibres turn sharply and wind in a counter-clockwise direction over the heart surface (fig. 3). At the apex (fig. 2) the muscle fibres again turn sharply and pass into the interior of the left ventricle. In so doing they form a vortex, not unlike that of mammals. The vortex (fig. 2) is easily separable into a dorsal and a ventral horn. The fibres that arise from the dorsal aspect of the heart base (between *A* and *B* in fig. 1) sweep around the right ventricle and form the ventral horn. Those which arise from the ventral side of the base (between *A* and *C* in fig. 1) sweep around to the left and form the dorsal horn. Using Mall's terminology, the

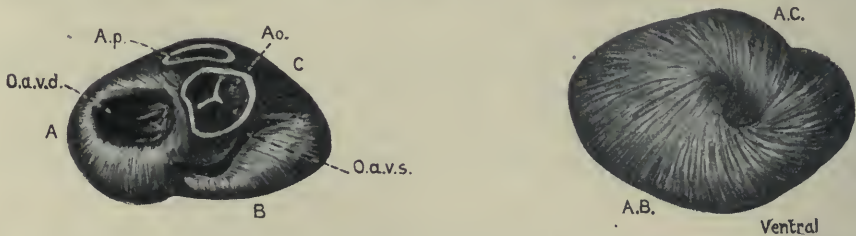


Fig. 1. Base of fowl heart.  $\times 1\frac{1}{2}$ . *A.B.* sino-spiral muscle; *A.C.* superficial bulbo-spiral muscle; *Ao.* aorta; *A.p.* Pulmonary artery; *O.a.v.d.s.* right and left atrio-ventricular openings.

Fig. 2. Apex of fowl heart.  $\times 1\frac{1}{2}$ .

two groups of fibres can be named the *sino-spiral* and *superficial bulbo-spiral* muscles, respectively. The sino-spiral muscle arises chiefly from the right atrio-ventricular ring and is to be associated with the sinus portion of the heart. The superficial bulbo-spiral muscle arises from the ventral side of the heart base, and is to be associated with the aortic and pulmonary orifices—the bulbar portion of the heart. From that part of the base between *B* and *C* in fig. 1 arises fibres that pass as flat curves laterally over the right ventricle or which go to join either of the two chief muscles. They can be considered as a special part of the sino-spiral muscle, concerned with the right ventricle.

To dissect, make a longitudinal incision not more than one millimetre deep on the dorsal surface, beginning at the cleft which separates the two horns of the vortex and then following the general direction of the fibres (fig. 3). Carefully peel away both flaps, freeing them from the base of the heart (fig. 4). The left flap should be freed for only a very short distance. The peeling off of the right flap will soon be stopped by a stout band of muscle (*V.a.v.d.* in fig. 4).



The right flap is made of sino-spiral muscle. It carries with it the ventral horn of the vortex. The sino-spiral fibres form also the basal two-thirds of the left flap; but the apical third is made of the superficial bulbo-spiral muscle, which can now be seen to pass *via* the dorsal horn into the newly exposed deeper portions of the bulbo-spiral muscle.

Return to the right flap. To peel it off any farther the stout muscle band (*V.a.v.d.* in fig. 4) must be cut across. With the further peeling of the flap the endocardium of the right ventricle tears, exposing the cavity of that ventricle (fig. 5). The medial wall of the right ventricle remains attached to the left ventricle, and the heavy muscle band which composes it (*L.v.d.* in fig. 5) locks with the sino-spiral muscle of the right flap, and stops the peeling process for a second time.

The nature of the muscle band just cut can now be realised. It forms the right atrio-ventricular valve (*V.a.v.d.* in figs. 4, 5, 6, 7)—a fleshy crescentic

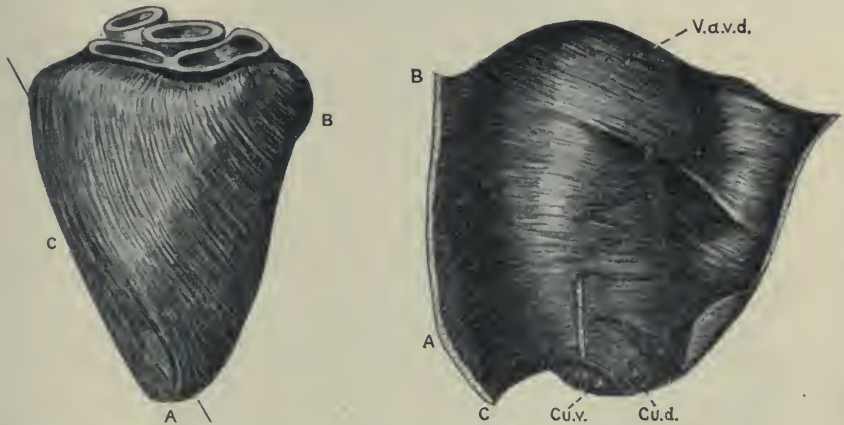


Fig. 3. Dorsal surface of fowl heart.  $\times 1\frac{1}{2}$ . A.B.C. as in Fig. 1.

Fig. 4. Fowl heart. First stage of dissection.  $\times 1\frac{1}{2}$ . A.B. sino-spiral muscle; A.C. superficial bulbo-spiral muscle; Cu.d. dorsal horn of vortex; Cu.v. ventral horn of vortex; V.a.v.d. right atrio-ventricular valve.

leaflet peculiar to the bird heart. Its fibres partially embrace the base of the left ventricle and merge with the other muscle bundles on the ventral and dorsal surfaces of the heart base. In such a way an extremely effective valve is formed. The more vigorous the general contraction of the heart, the more firmly the right atrio-ventricular orifice is shut.

As already stated, the medial wall of the right ventricle is formed by a great longitudinal band (*L.v.d.* in fig. 5) which at this stage of the dissection locks apically with the sino-spiral muscle. This *longitudinal muscle of the right ventricle* arises from all sides of the aorta, except that in contact with the left atrio-ventricular orifice. It passes spirally over the ventral surface of the left ventricle, and merges with that part of the superficial bulbo-spiral muscle which is cut in fig. 4. Its further course is that of the superficial bulbo-spiral muscle.

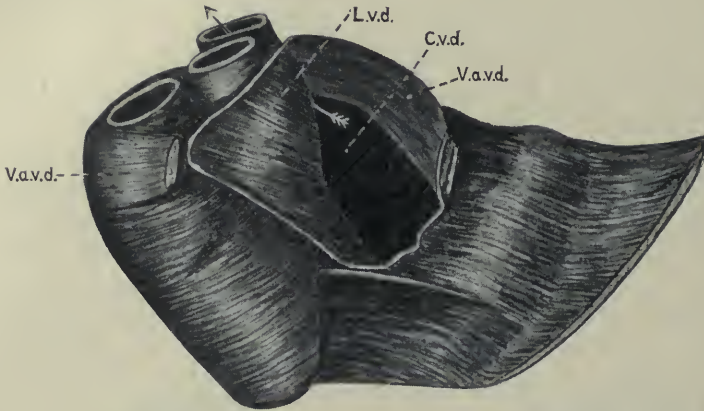


Fig. 5. Fowl heart. Second stage of dissection.  $\times 1\frac{1}{2}$ .  
(Lettering as in Fig. 4.)

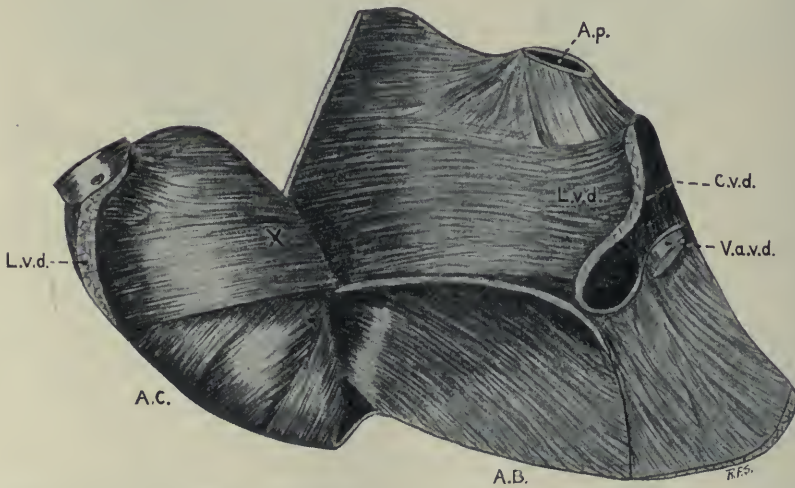


Fig. 6. Fowl heart. Third stage of dissection.  $\times 1\frac{1}{2}$ . *A.B.* sino-spiral muscle; *A.C.* superficial bulbo-spiral muscle; *A.p.* pulmonary artery; *C.v.d.* cavity of the right ventricle; *L.v.d.* longitudinal muscle of the right ventricle; *V.a.v.d.* right atrio-ventricular valve; *X* deep bulbo-spiral muscle.

To peel off the right flap farther the longitudinal muscle of the right ventricle must now be cut near its origin. The right and left ventricles will then separate (fig. 6), the ventral horn of the vortex will then be completely unrolled, and the sino-spiral muscle can be seen to pass into the left ventricular cavity beneath the superficial bulbo-spiral muscle.

When the left ventricle is unrolled as far as this stage of the dissection will permit (fig. 6) the internal portions of both the sino-spiral and superficial bulbo-spiral muscles will be found to be locked with a third band, which arises beneath both muscles and covers their internal portions. This third band (*X* in fig. 6) can be called the *deep bulbo-spiral* muscle. In so far as it has any fixed origin, it arises beneath the superficial bulbo-spiral muscle. Its fibres

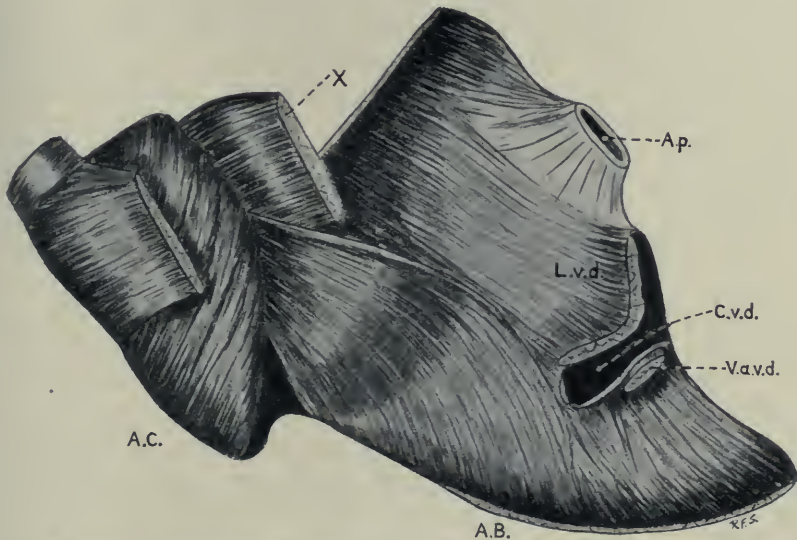


Fig. 7. Fowl heart. Fourth stage of dissection.  $\times 1\frac{1}{2}$ . *A.B.* sino-spiral muscle; *A.C.* superficial bulbo-spiral muscle; *A.p.* pulmonary artery; *C.v.d.* cavity of the right ventricle; *L.v.d.* longitudinal muscle of the right ventricle; *V.a.v.d.* right atrio-ventricular valve; *X.* deep bulbo-spiral muscle.

form a closed ring, or hood, around the basal part of the left ventricle. Beneath the aorta, the deep and superficial bulbo-spiral muscle fibres blend rather intimately, and at all places the fibres of the deep muscle pass into the underlying parts of the superficial bulbo-spiral and sino-spiral muscles.

To display the deeper portions of the last two, it is necessary to cut across the deep bulbo-spiral muscle. When this is done, the left ventricle can be unrolled almost into a flat sheet (fig. 7). When the more or less circular deep bulbo-spiral muscle is pulled aside, one finds that the terminations of the two superficial muscles form an internal sheet, whose fibres run at right angles to the outer one. The sino-spiral fibres pass into the ventricle and form most of its inner wall. Groups of fibres project to form the small papillary muscles; the majority after partly encircling the ventricle, end along the atrio-ven-



tricular ring. The superficial bulbo-spiral muscle forms a quite distinct band, shown in fig. 7, which wraps around the terminal fibres of the sino-spiral muscle, sweeps around the right side of the ventricle, and ends very largely at the root of the aorta. The two muscles form an internal investment for the left ventricular cavity which is complete on all sides save the left. There the separation of the horns of the vortex produces a definite cleft. If the termination of the superficial bulbo-spiral muscle is cut from its attachment to the root of the aorta, the left ventricle can be unrolled into practically a flat sheet of muscle.

It may be pointed out here, that the right ventricle is hardly more than a cleft between the longitudinal muscle of the right ventricle, i.e. the bulbo-spiral muscle, and the sino-spiral muscle. Its lateral wall is made up of the more circular fibres which arise between *B* and *C* in fig. 1, which are shown in part in fig. 3, and the fleshy valve of the ventricle already discussed. The inner surface of the right ventricle is perfectly smooth—there are no papillary muscles of any kind.

The anatomy of the bird heart is, then, the anatomy of the left ventricle, and the muscles which form its walls are of two groups:

1. Sino-spiral group:

Sino-spiral muscle,

Muscle of the right atrio-ventricular valve.

2. Bulbo-spiral group:

Superficial bulbo-spiral muscle,

Longitudinal muscle of the right ventricle,

Deep bulbo-spiral muscle.

The sino-spiral muscle arises from the dorsal segment of the heart base. The chief mass of its fibres passes superficially and spirally to the apex, where they form the ventral horn of the vortex. The fibres pass into the heart, form most of the internal wall of the left ventricle, and pass spirally up toward the heart base. The fibres which do not form papillary muscles end along the left atrio-ventricular ring.

A smaller group of fibres from the same general origin passes to the right in a roughly circular course, and constitute the lateral wall of the right ventricle.

The muscle of the right atrio-ventricular valve can be considered as a special part of the preceding. Its fibres arise beneath the sino-spiral group on the dorsal side of the left ventricle and end on its ventral aspect, beneath the superficial bulbo-spiral muscle.

The superficial bulbo-spiral muscle arises from the ventral segment of the heart base, and passes spirally to the apex, where it forms the dorsal horn of the vortex. From this point the fibres turn upwards, and course spirally between the deep bulbo-spiral muscle without and the sino-spiral muscle within to the root of the aorta.

The longitudinal muscle of the right ventricle is at once the medial wall of that ventricle, and a part of the bulbo-spiral muscle of the left. It arises

from the root of the aorta, winds apically over the ventral surface of the left ventricle and then joins the superficial bulbo-spiral muscle.

The deep bulbo-spiral muscle is in the main a closed ring which surrounds the termination of the superficial muscles. It is the middle circular band of Pettigrew and others. Whatever fixed origin it has is beneath the superficial bulbo-spiral muscle. As in mammals, it varies greatly in development. In the Mallard duck it forms a very definite ring; but in many fowls it is hard to separate from the other bands.

As Pettigrew long ago pointed out, the hearts of mammals and of birds are very much alike. A comparison of the drawings of this paper with those of Mall will bring home the great similarity. Evidently like mechanical needs have been met by like structural arrangements. The lesser development of papillary muscles in the left ventricle of the bird makes a difference which is more apparent than real, for a papillary muscle is, after all, but a split off portion of the ventricular wall. The muscular valve of the bird's right ventricle, although perfectly characteristic, is after all only a highly developed portion of the sino-spiral muscle which here winds circularly around the heart base in both classes. The longitudinal muscle of the right ventricle is far better developed in birds than in mammals, and shows its relation to the bulbo-spiral muscle much more clearly than in the human heart. In man, Mall was led to include it in the sino-spiral system, despite its typically bulbar origin.

The avian heart muscle, taken as a whole, forms a sheet folded into a figure 8. It is made of two spiral S-shaped segments, one superficial and one deep. The two portions are continuous at the heart apex; at the base, however, they do not unite as the figure 8 would suggest. When the heart contracts, each S-shaped segment shortens, and the blood is literally wrung out of the ventricular cavity. Such a contraction process is of course identical with that of the mammal, first figured by Borelli (1681).

#### HEARTS WITH ONE VENTRICLE

The hearts of the fish, amphibian, and reptile form a roughly graded series of increasing complexity, which can best be described by beginning with the simplest. As representatives of each class, I have chosen the lake or rock sturgeon, *Acipenser rubicundus*, from Lake Nipigon, Ontario; the leopard frog, *Rana pipiens*, widely used in physiological laboratories; and the turtle, *Emys blandingii*, likewise a common laboratory animal. All hearts were fixed and preserved in carbolic acid. Soaking in dilute acetic acid overnight is enough to prepare the fish heart for dissection; the others require no preliminary treatment, other than thorough washing. In all cases, dissection was constantly checked with serial microscopic sections cut in all three planes.

*Fish.* The sturgeon heart is provided with a large conus arteriosus, the musculature of which is quite distinct from that of the ventricle. The conus consists chiefly (figs. 9 and 10) of a heavy external circular coat. Between it and the thick connective tissue intima can be found a thin longitudinal muscle

layer. From the atrium there passes down into the ventricle, a thin layer of scattered muscle fibres which are embedded in the connective tissue of the atrial canal, and which join the major strands on the inner wall of the ventricle.

If the fat is removed with great care the thin *superficial muscle* sheet can be identified (fig. 8). Its fibres form a sort of sling for the heart apex. They arise from the root of the conus and the adjacent part of the atrio-ventricular ring, and end on the same ring on the opposite side.

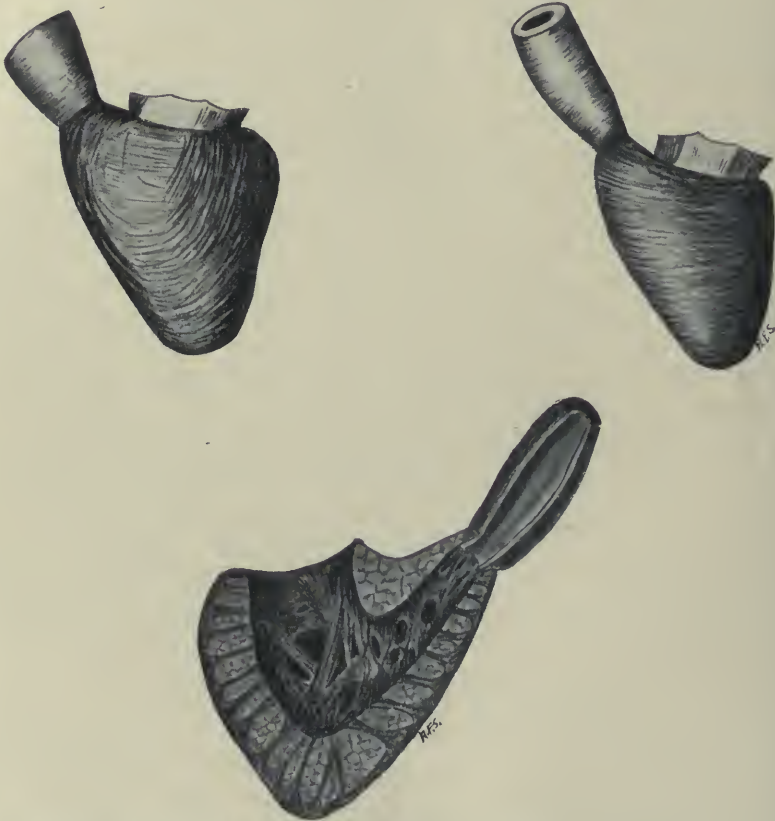


Fig. 8. Heart of sturgeon (*Acipenser rubicundus*). Superficial muscle layer.  $\times 1\frac{1}{2}$ .

Fig. 9. Heart of sturgeon (*Acipenser rubicundus*). Circular muscle layer.  $\times 1\frac{1}{2}$ .

Fig. 10. Frontal section of sturgeon heart (*Acipenser rubicundus*). Dorsal view.  $\times 1\frac{1}{2}$ .

When the superficial sheet is removed, the external *circular coat* comes into view. This coat (fig. 9) is made of fibres whose general course is circular; that is, they run around the cone-shaped ventricle for variable distances. The layer is thickest at the atrio-ventricular orifice. The circular layer cannot be dissected off with any success, for its component fibres run in it for very short distances, and then dip into the deeper layer, from which they arise. A better idea of the deeper layer can be got from a section such as shown in fig. 10.



The innermost, and chief part of the ventricular wall, is a closely woven muscular basket. Its bottom forms the apex of the heart. Above there are two openings, at each of which the strands of the basket are gathered into great cylindrical sheets. At the conus orifice, the fibres are attached to the intima of the conus, or continue in part into the longitudinal muscle layer of the conus. At the atrial orifice, the fibres pass in great strands over its lip out on to the ventricular surface. The strands pass out at various angles; any definite spiral direction such as appears in the turtle cannot be found in the fish.

From all parts of the basket smaller strands pass out to form the circular layer already described. Any such offset can be seen in microscopic transverse section to approach the surface at right angles to it, and to divide into two or more circularly running strands. The latter make up the circular layer, and after a longer or shorter course again dip into the deeper basket layer.

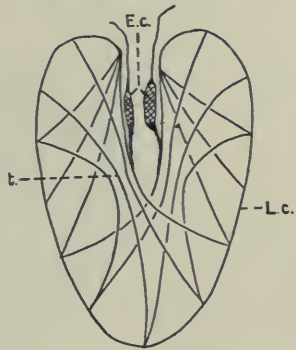
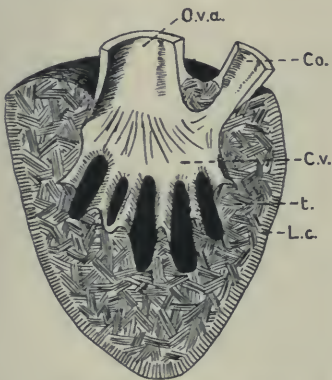


Fig. 11. Heart of frog (*Rana pipiens*). Frontal section. Dorsal view.  $\times 7\frac{1}{2}$ . Co. conus; C.v. cavity of the ventricle; L.c. circular layer; O.v.a. atrio-ventricular opening; t. trabecula.

Fig. 12. Heart of frog. Diagrammatic sagittal section. E.c. endocardial cushion; L.c. circular layer; t. trabecula.

The heart of the sturgeon, as above described, is almost exactly like that of the salmon as given by Pettigrew.

*Frog.* In the frog heart, no superficial layer such as appears in the sturgeon can be seen. The circular layer, which comes into view as soon as the pericardium is stripped off, is very much like the same layer in the fish (fig. 9). It is thinner—not more than one cell thick in these small hearts—and can best be described as a syncytial meshwork, the cells of which take a generally circular direction.

The chief structure of the frog heart, as of the fish, is an internal muscle basket. From the basal half of the ventricular surface spring numerous muscle strands. These group into two sheets, placed along the ventral and dorsal margins of the atrio-ventricular orifice. A frontal section (fig. 11) displays the ventral sheet. Each sheet divides into six or more trabeculae. The trabeculae branch, anastomose, inter-digitate, and form a dense and confusing

basket wall, which fills most of the ventricular cavity. From every part of the basket, slender offsets pass to the surface, continue for varying distances as components of the circular layer, and then dip back again into the underlying basket.

The muscular basket, although much like that of the fish, is somewhat better organised. The fibres do not run so irregularly. Their course can be worked out in serial sections. Fig. 12, a composite diagrammatic sagittal section, shows their general direction and distribution.

The free cavity of the frog ventricle is lined with a continuation of the atrial wall, the connective tissue of which thickens along the ventral and dorsal margins into two pearly white pads (fig. 12). The pads are not present in the sturgeon, but they reappear in the turtle. They seem to correspond to the endocardial cushions of the embryonic heart of the bird and mammal, and may be given the same name.

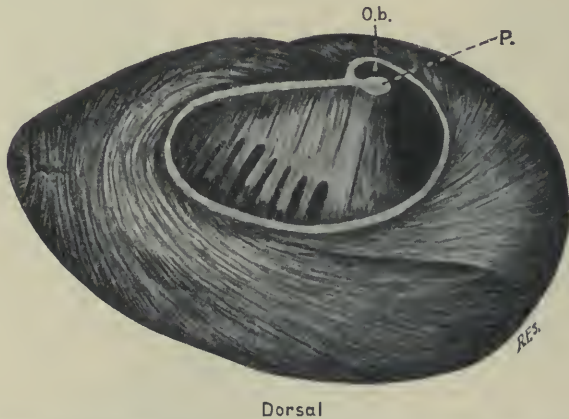


Fig. 13. Heart of turtle (*Emys blandingii*). Dorsal view.  $\times 2$ . O.b. bulbar orifice; P. large ventral trabecula.

*Turtle.* In the turtle, the slight amount of cardiac muscle that separates the atrial and bulbar orifices in the frog, disappears. The base of the heart is edged with a connective tissue collar, which is divided by a sort of bridge into atrial and bulbar openings. Each of these are secondarily subdivided; the atrial into two, and the bulbar into three orifices. Within the heart, along the ventral and dorsal sides, the collar bears large endocardial cushions.

In passing, it may be pointed out that the atria of the turtle heart are lined with a layer of smooth muscle, which passes down through the atrial canal into the ventricle. The nature and extent of this peculiar layer has been described elsewhere (Shaner, 1923).

To show the course of the ventricular musculature, the atria and the bulbar arteries must be cut away, the two openings made into one by cutting away the bridge which separates them, and the endocardial cushions removed. The ventricle then appears as in fig. 13.

The interior of the ventricle is lined with almost perpendicular trabeculae. From the oblong shape of the ventricle, the trabeculae naturally group themselves into two sets, which can be called the ventral and dorsal groups respectively. In the drawing only the ventral set is shown; the dorsal set is quite like it.

Both groups of trabeculae arise in the meshwork at the bottom of the ventricle, and pass upwards around the connective tissue collar. The fibres of the ventral trabeculae pass out along the ventral segment of the heart base on to the surface, turn spirally around to the left in a counter-clockwise direction, and spread out over the dorsal surface of the ventricle. In the same fashion the fibres of the dorsal trabeculae pass out to the right and cover the ventral surface and the keel-like apex of the ventricle. If a shred of muscle be picked up as it leaves the ventral trabeculae, it can be followed around the left shoulder of the ventricle on to the dorsal surface. There the fibres spread out, and end at various distances by passing into the depths and joining a dorsal trabecula. In the same way fibres of the dorsal trabeculae, as they pass over the ventral surface, end irregularly in one of the ventral trabeculae; or, if they run along the keel of the heart, end in either set of trabeculae without any special arrangement.

The trabecula, which stands at the extreme right of the ventral series in the figure, is much larger than the rest, and stands like a pillar in the ventricular cavity, which it partially subdivides. Many of the fibres that compose it run up into the bulb, and are inserted in a little piece of cartilage (the ossiculum cordis of Bojanus), to which are attached the medial valves of the bulbar arteries.

The fish and frog heart are much alike. Both are made of a circular outer and a longitudinal inner coat, the first of which contracts the transverse, and the second the longitudinal dimension of the conical ventricle. The ventricular cavity is squeezed somewhat like the bulb of a camera shutter.

The turtle heart offers an interesting intermediate condition, in both structure and function. In its general simplicity of make-up, the turtle is but slightly removed from the ichthyopsidan ventricle. The chief structural advance is the spiral arrangement of the surface fibres, which at once suggests the bird and mammal. The large ventral trabecula of the turtle, which anchors the bulb and ossiculum cordis, may be related to the longitudinal bundle of the right ventricle in higher forms. When the heart contracts, there can be seen a distinct twisting, somewhat like that of the bird and mammal.

In general the hearts of vertebrates fall into two classes, the ichthyopsidan and the bird-mammal class. The distinction is not absolute, for the turtle heart is intermediate, and other reptiles, especially the alligator and crocodile, may bridge the gap still further. In the absence of embryological evidence, the relation of the two classes is difficult to make out. Speculation would be interesting, but it is wiser to wait until the technical difficulties that bar the way to the study of the embryonic musculature are surmounted.



*Note.* My efforts to work out the embryology of the heart musculature have so far been balked by technical difficulties. Pig embryos were stained with Mallory's phosphotungstic acid haematoxylin, to bring out the myoglia fibrils, with the hope that these would serve to indicate the direction of the muscle cells. But the obliquity of such fibrils cannot be measured in serial sections.

As one passes through the sections of the heart of a 12 mm. pig embryo, he finds a suggestive resemblance to the adult heart of the turtle. One other very curious fact was noted. The cardiac muscle of the 12 mm. pig embryo is already fully striated—at a time when all other muscle is still undifferentiated mesenchyma.

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## ON THE SEXUAL AND RACIAL CHARACTERS OF THE HUMAN ILIUM

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THE work upon which this paper is based was undertaken in the first instance with the idea of showing that certain characters of the human ilium visible to the eye and of value to the anatomist, as aids in sexing the bone, might also be measured, and so be of interest to the statistician. But as the work proceeded it became evident that the influence of race had such an important bearing on the question that it was impossible to ignore it. In the following account which deals with measurements on the English hip-bones from the Whitechapel plague pits as well as bones from different periods in Egypt, and certain hip-bones from Dr Geo. Reisner's excavations at Kerma in the Sudan, the various groups mentioned are dealt with separately.

The results of the measurements obtained from the ilium justify us in considering this portion of the hip-bone to be of great sexual importance, while the racial factor appears to be of sufficient influence to necessitate the rigid separation of the different groups.

At the outset a word must be said with regard to the sexing of the material.

All the bones were sexed by means of the various features which experience has shown to be of the most value, and *before* any measurements were made. Objection has been taken to the fact that as we are measuring and comparing the very characters which we have previously employed as indicative of sex, and having segregated the bones according to these characters, we should naturally find them emphasised in the measurements. This is fair criticism and it follows that the only absolutely exact method of carrying out such an investigation would be to employ only those bones which have been taken from bodies of known sex. However no series such as Wingate Todd has collected is accessible to me, consequently we must either accept the anatomical verdict of sex for the great majority of the bones employed, or lose a large amount of material the sex of which can never be known with absolute certainty.

Most of the bones measured for the present work came under the latter category, but a few pelves were obtained from mummies in which the sex was known either from names on the tombs or coffins, or from the preservation of the organs. In none of these, when the hip-bones themselves came to be examined, were the features chosen as characteristic of sex falsified, and the series forms therefore a valuable corroboration of the correctness of the methods employed in sexing. Nevertheless, as already stated above, none of

the measurements presently to be detailed, were employed in sexing the bones, this being done entirely by ocular appreciation of all the characters concerned. This is an easier task in the case of the hip-bone than in that of any other bone in the skeleton, because sexual function in the woman has impressed upon the bone features, which if not absolutely peculiar, are so much more pronounced in her sex, as to leave no doubt in the great majority of cases, concerning the sex of the individual to whom the bone belonged.

In comparing typical male and female hip-bones it will be noticed that the great sciatic notch, or ilio-sciatic notch as it is better termed, differs markedly in the two sexes. In the man (fig. 1) the margins of the notch enclose a relatively deep and narrow excavation; in the woman (fig. 2) the posterior margin slopes backwards in such a way as to form a wide shallow arch in

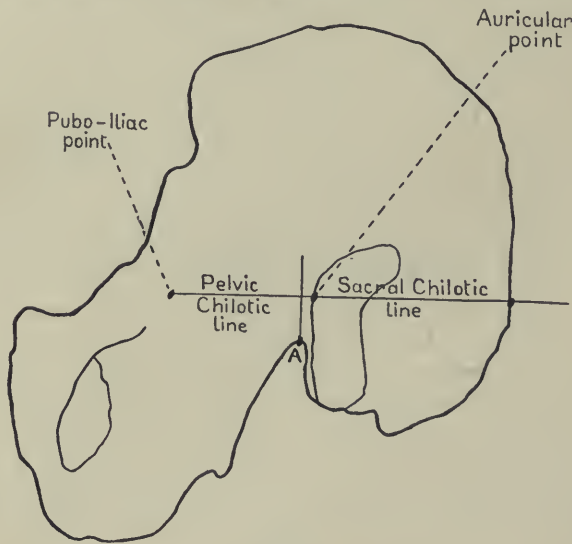


Fig. 1

striking contrast to that in the male. This difference in shape is associated with a difference in the position of the articular surface for the sacrum, and therefore of the sacrum itself, such that it stands further back in the pelvic cavity in the woman thus increasing the antero-posterior diameter of the pelvis. This implies a greater length of the iliac part of the ilio-pectineal line in women, and in conjunction with this there is a lessening in the extent of the rough area behind the auricular surface. These are well-recognised sexual characters and it remains to select suitable points from which to measure them.

For this purpose two points are chosen. The first is situated on the ilio-pectineal line at the site of the original union of the os pubis and ilium, and may be called the *pubo-iliac point* (fig. 1); the second is on the anterior margin of the auricular articular surface where this approaches nearest to the pubo-iliac point, and is termed in the present paper the *auricular point*. As the



correct identification of the pubo-iliac point in every hip-bone to be measured is essential for an accurate comparison of the characters under consideration, a more detailed explanation of the method employed in finding it is necessary.

*Pubo-iliac point.* In the large majority of adult hip-bones the original lines of union of the three constituent parts of the bone are obliterated, but a careful examination of hundreds of bones has shown that very fair accuracy may be obtained in identifying these lines if the following method is used:

The original lines of union of the ischium with the os pubis on the one hand, and with the ilium on the other are often faintly visible on the pelvic surface of the bone. These two lines meet at a point just below the ilio-pectineal line and the continuation from here of the old line of junction across the brim of the pelvis can frequently be detected. When this is the case a small dot should be marked with a pencil on the ilio-pectineal line at the point where it is crossed by the faintly-marked original line of union of the ilium and the os

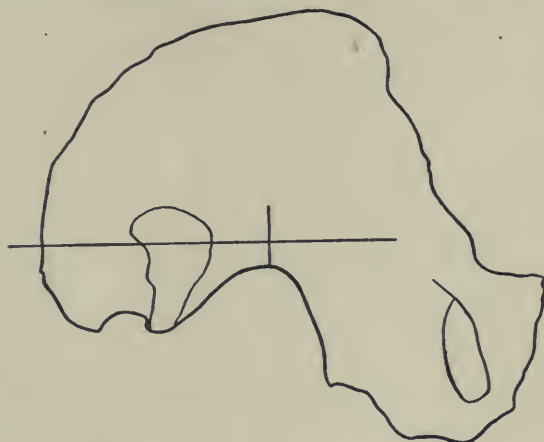


Fig. 2

pubis. If this is correctly done it will be found that the pencil mark is immediately opposite the deepest part of a depression in the acetabular rim. In many bones this notch in the rim is very pronounced and it also represents the place where the os pubis and ilium united. By this means therefore a double check on the true position of the pubo-iliac point is obtained. At times however it is impossible to detect any trace whatever of the line of union, and in such cases a line should be drawn from the notch in the rim of the acetabulum at right angles to the axis of this part of the ilium, the pencil dot being placed on the ilio-pectineal line, where the latter is cut by the line from the acetabulum. A further guide to the line of union is found in the fact that the bone here is very slightly elevated, and if it is held up to the light on a level with the eyes, the faintly-marked eminence produced by the original junction of the os pubis and the ilium can usually be detected. When the pubo-iliac point has been marked on the bone, the point on the margin of the auricular surface where the latter approaches nearest to the pubo-iliac point can be

easily determined with dividers and the *auricular point* so found similarly indicated by a pencil dot.

All the measurements here recorded have been made from projection drawings of the bones after setting them up in the manner now to be described.

The instrument used for tracing the outline of each bone was Martin's projection apparatus. The hip-bone is laid on the board beneath the glass table and is then manipulated with the aid of a wedge introduced under the bone until the two points *pubo-iliac* and *auricular* are on exactly the same level. This is determined by means of a scriber, whose pointed turned down arm is adjusted over each pencil spot in turn until the two are found to be on precisely the same horizontal line. As soon as this is done the drawing can be made. The two points should be indicated first, and then the whole bone should be traced out. The tracing should include an outline of the sacral articular surface.

When the drawing is complete the two points already indicated are united by a line which is produced posteriorly until it crosses the iliac crest. This line in its anterior part corresponds fairly closely with the iliac portion of the ilio-pectineal line, and thus with the pelvic brim. For this reason the whole line from pubo-iliac point to the place where it crosses the iliac crest has been termed the *Chilotic line* from the Greek χείλος (a brim or lip). It consists of two main parts, an anterior or pelvic portion between pubo-iliac and auricular points, and a posterior or sacral portion extending from the last-named point to the iliac crest. For the sake of brevity these two portions of the Chilotic line will be called throughout this paper Pelvic Chilotic and Sacral Chilotic respectively (see fig. 1).

One more point of great importance must now be indicated on the drawing. This is the apex of the ilio-sciatic notch or more accurately that part of the ilio-sciatic arch which approaches nearest to the Chilotic line (see *A* in fig. 1). A pencil mark is made on the drawing at the required spot, and from this point a line is drawn upwards cutting the Pelvic Chilotic line at right angles (see fig. 1). This portion of the Chilotic line is therefore divided into *two segments*, anterior and posterior, lying on either side of the line drawn from the highest part of the ilio-sciatic notch.

#### MEASUREMENTS

The Chilotic line as a whole and the parts into which it has been divided as described above can now be measured. In the first place the length of the two main portions, pelvic and sacral, is found and the relation of Pelvic Chilotic to Sacral Chilotic line gives the *Chilotic Index* =  $\frac{\text{Sacral Chilotic} \times 100}{\text{Pelvic Chilotic}}$ .

When these two portions of the total Chilotic line are of equal length the Index will of course be 100, and this figure may be taken in a general way to represent the boundary line between the sexes, a *typical* female having an index below 100, a *typical* male being invariably above that figure.

As will be shown later on in this paper this broad generalisation has to be considerably modified for the women: but as the essence of the investigation turns on the fact that the Pelvic Chilotic line in women is not only actually greater than that in men, but also, in many cases in the female, greater in relation to the Sacral Chilotic portion, the introduction of the statement at this stage is justified.

The next step is to find the lengths of the two segments of the Pelvic Chilotic line. These are situated as already described on either side of the Vertical line drawn from the apex of the ilio-sciatic notch. The relation of these two measurements is expressed as follows:

$$\frac{\text{Posterior Segment of Pelvic Chilotic line} \times 100}{\text{Anterior Segment}}$$

= *Chorematic Index*, a term derived from the Greek word χώρημα (space, room) because the Index is a measure of the proximity or otherwise of the sacral articular surface, and therefore of the sacrum, to the ilio-sciatic notch, with a consequent alteration in the capacity of the true pelvis.

#### MATERIAL

It has already been mentioned that the measurements as just detailed have been carried out on the English hip-bones from Whitechapel now in the care of the Biometric Department at University College, London, but formerly belonging to Sir George Thane, to whom the thanks of the writer are due for the loan of this valuable material. In addition a number of hip-bones of the Vth–XIIth Egyptian Dynasties 2500–2000 B.C. have been measured as well as some from the Predynastic era and a few from Dr Geo. Reisner's excavations at Kerma in the Sudan<sup>1</sup>. It is to be regretted that a number of measurements made on bones from the Collection of the Archaeological Survey of Nubia have had to be discarded owing to their mixed origin, and the smallness of the numbers that a separation into racial groups would entail.

#### CHILOTIC INDEX

The results obtained from the measurements may now be considered.

Table I. *Men*

Race	No.	Chilotic line		Total length	Chilotic Index	Pelvic Chilotic line		Chore-matic Index
		Pelvic portion	Sacral portion			Antr. segment	Postr. segment	
English ... ..	61	52.8	71.2	123.9	136.1	48.9	3.9	8.2
VIth–XIIth Dyn.	42	55.0	68.4	123.2	125.9	49.8	5.6	11.5
Predynastic ...	24	54.5	67.7	122.2	125.6	46.1	8.1	18.7
Kerma ... ..	19	55.5	68.4	123.9	125.2	45.8	9.8	21.8

<sup>1</sup> The Kerma crania which were measured by the writer in 1920 are almost identical with the Middle Nubian people described in the *Bulletins of the Archaeological Survey of Nubia*. The nasal measurements, however, indicate a greater infusion of negro blood than was found to be the case in the Middle Nubians. The negro influence is emphasised in the pelvic measurements.



As will be seen in the accompanying Table I, the *total length* of the Chilotic line in the men is practically identical in three out of the four groups examined. There is in fact no sensible difference in the actual size of the bone in these races. But a remarkable difference is apparent in the English men as compared with the other three groups when the Chilotic line is divided into its two component parts Pelvic and Sacral. In this case the English are found to have the shortest Pelvic Chilotic line (52·8) as against an average of 55·0 in the remaining groups, but they have at the same time the longest Sacral Chilotic line (71·2) so that the *Chilotic Index* for this race rises to 136·1.

Table II. *Women*

Race	No.	Chilotic line		Total length	Chilotic Index	Pelvic Chilotic line		Chore-matic Index
		Pelvic portion	Sacral portion			Antr. segment	Postr. segment	
English ... ..	34	55·7	61·3	117·0	110·8	44·8	10·9	24·7
VIth-XIIth Dyn.	32	62·9	56·5	119·5	90·7	46·5	16·5	36·1
Predynastic ...	42	59·0	63·1	122·3	107·1	46·3	12·6	27·8
Kerma (Nubian)	21	60·9	62·1	123·0	103·2	48·3	12·6	26·8

In the women (Table II) the *total length* of the Chilotic Line varies from 117·0 in the English to 123·0 in the Kerma group. But although the Pelvic portion of the line is again shorter in the English women than in the women of the other groups, in all of them it *exceeds* the length of the same line in the men of their respective races (see Table I). This is of course only another way of demonstrating the greater antero-posterior diameter of the pelvis in women. When, however, we come to examine the *Sacral Chilotic* line in this sex we find it to be consistently smaller than in the men, both actually as well as in relation to the total length, so that the Chilotic Index falls towards the figure already suggested as the boundary line between men and women, *i.e.* 100, and in the VIth-XIIth Dynasty Egyptian women reaches as low as 90·7. It is instructive to note, however, that as in the case of the English men, the Whitechapel women have the highest Chilotic Index. The significance of this will be discussed later.

#### CHOREMATIC INDEX

We may now examine the relation of the two segments of the Pelvic Chilotic line to each other. Beginning again with the English men (Table I), we find that the division of this line in the manner described above, yields a mean of only 3·9 mm. for the posterior segment. This means that the most anterior point on the margin of the sacral articular surface is only 3·9 mm. from the line drawn upwards from the highest part of the ilio-sciatic notch. The shortness of the Pelvic Chilotic line in the English men is thus explained, and is seen to be due to the advance of the sacrum which is nearer to the notch in this race than in any of the others measured. As a consequence the Chorematic Index is very low (8·2), and is approached only by the Old Empire Egyptians with an Index of 11·5. In the two remaining races the Chorematic

Index is relatively high, but in both of these the posterior segment of the Pelvic Chilotic line is more than double the length of that in the English owing to the sacrum standing further back from the notch, a condition which is associated with a more erect position of the sacrum and absence of the sacro-vertebral angle.

It should be noted that the race with the lowest Chorematic Index (8.2) has the highest Chilotic (136.1) and in general it may be said that these two Indices stand in inverse ratio to one another.

In the women the *Chorematic Index* is in marked contrast to that in the men. Although the English women are the lowest of the four female groups in this regard, their Index (24.7) is nevertheless three times as large as the Chorematic Index in English men. The explanation is the same as that given above for the men, and is due to the posterior segment of the Pelvic Chilotic line being so much longer in women than in men. Fig. 2 shows an outline of a female hip-bone in which the sacral articular surface is well removed from the vertical line (cf. Fig. 1). This is the typical female condition and all the groups illustrate it, but none so well as the Egyptian women of the Old Empire in whom the Chorematic Index rises to 36.1, as compared with 11.5 in the men of the same period. Here again too we find that the highest Chorematic Index is associated in the same race with the lowest Chilotic Index 90.7.

In the two remaining female groups, Predynastic and Kerma, the Chorematic Index, although high, does not exhibit the remarkable contrast to the men of their own race which is illustrated in the two higher races. In these two primitive groups there is a tendency towards greater similarity between the sexes in this regard, thus confirming by measurement, what had been encountered in sexing these hip-bones by the ordinary anatomical methods, viz. that sexual differences in primitive races are less marked than in the higher races. This is brought out in the Tables I and II, where the lengths of the posterior segment of the Pelvic Chilotic line in the two sexes of the Predynastic and Kerma groups, are much nearer to one another than in the English and Old Empire Egyptians with a resulting similarity in the Chorematic Index.

We may now consider in more detail the meaning of the remarkable differences which we have found to exist, as between the sexes, in this (iliac) part of the hip-bone. For this purpose it is necessary in the first place to examine the same region in some of the lower animals. We have seen that the essential difference in the human ilium between men and women is in the position of the sacral articular surface, which by its greater or less distance from the line drawn upwards from the apex of the ilio-sciatic notch, increases or lessens the posterior segment of the Pelvic Chilotic line. The position of the articular surface is of course the position of the sacrum and accordingly the antero-posterior diameter of the pelvis varies with it. Now in most of the lower animals this antero-posterior diameter is very long, the sacrum standing far back from the symphysis pubis, while the ilio-sciatic notch, which is such

a well-marked feature of the human hip-bone, is non-existent as a notch, and is represented only by a shallow excavation of the ilio-sciatic border. This is the condition with very slight variations in practically all the Mammalia. In the Apes (Fig. 3) we begin to find indications of a notch and this is due to a



Fig. 3

slight downward bending of the ilium in the neighbourhood of the sacral articular surface. The hip-bones of the Anthropoid-Apes furnish a good illustration of this commencing notch which only reaches its characteristic form in man. That this is directly related to his erect carriage, seems to be the natural corollary.

This conclusion is borne out by the following facts. The posterior superior iliac spine in man is approximately at the level of the spinous process of the second Sacral Vertebra and is only removed from the posterior inferior spine by a very short interval. The last-named "spine" is really the lower end of the sacral articular surface. Now if we examine the corresponding points in a baboon we find that the posterior superior spine lies altogether above the



Fig. 4

level of the sacral spines, on a level with the lower border of spine of last lumbar and is separated from the posterior inferior spine by a long straight border. This is strikingly demonstrated, if the hip-bone of this ape (Fig. 3) or of the orang (Fig. 4) is treated in the manner described in this paper for the



human bone. In such a case when the Chilotic line is drawn through the two points pubo-iliac and auricular and produced backwards to cut the iliac crest, it is found to pass *not* through the crest and *above* the posterior superior spine as in man, but *below* it, between posterior superior and inferior spines (see Figs. 3 and 4). The posterior superior spine as well as the posterior part of the ilium, must therefore have been dragged down in the human being in the process of walking erect and this has brought the sacrum down with it. But another influence has also been at work, viz. the body weight. This acting on the base of the sacrum has forced that bone forwards, so that while the sacrum as a whole has descended lower into the pelvic cavity by reason of the pulling down of the ilium, it has also moved towards the symphysis. Now the amount of this forward movement is measured, as we have seen, by the length of the posterior segment of the Pelvic Chilotic line, and this is short in the men and long in the women. But of the four racial groups, the English of both sexes

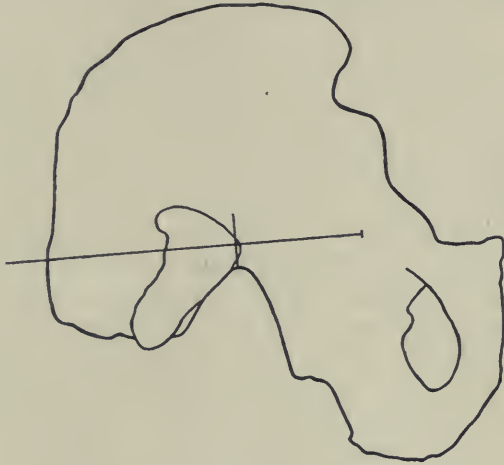


Fig. 5

exhibit the greatest amount of forward movement. This is most marked in the men, so that the mean length of the posterior segment of the Pelvic Chilotic line is reduced in this sex to only 3.9, while in five cases out of 61 this forward movement has been carried so far that the anterior margin of the sacral articular surface actually overlaps the line drawn from the top of the ilio-sciatic notch, thus reducing the posterior segment of the Pelvic Chilotic line to a minus quantity (see Fig. 5). This was never met with in any female bone measured.

In the hip-bones of the Egyptian men of the Vth-XIIth Dynasties much the same state of affairs exists. The posterior segment of the Pelvic Chilotic line is short (5.6) and there is an even larger percentage of cases where this line is reduced to minus. In the Predynastic Egyptians, and still more in the Kerma people, the posterior segment of the Pelvic Chilotic line is very definitely longer with a consequent rise in the Chorematic Index. In other words the

sacrum has not moved forward to the same extent as in the two higher races. For this reason, as mentioned above, there is greater similarity between the sexes in these more primitive people, while at the same time the smaller forward movement of the sacrum accounts for the greater frequency of the dolichopellic type of pelvis in primitive races.

In this connection it should be noted that the more upright position of the sacrum in the negro races is associated with a reduction in, or even complete absence of, the lumbar convexity. In these people the sacro-vertebral angle scarcely exists, and the antero-posterior diameter of the pelvis is therefore relatively long, thus recalling the shape of the pelvis in the apes. This is in marked contrast to the pronounced angle and prominent lumbar curve in such a race as the English, in whom, as has been shown, the antero-posterior diameter is shorter than in any of the racial groups examined in the course of this investigation.

Is it possible to give any explanation of these striking sexual and racial differences?

Some light seems to be thrown on the subject by the following facts. (a) In cases of rickety pelvis in women the impediment to normal labour is the reduction in the antero-posterior diameter or conjugate owing to the pushing downwards and forwards of the sacrum, by the body weight acting on abnormally soft bones. In these cases the hip-bones are of an exaggerated male type in regard to the ilio-sciatic notch and the backward bending of the ilium. (b) In an oblique pelvis in a woman due to congenital fusion of the right sacro-iliac joint with consequent lack of development of the ala of the sacrum on the same side, the affected side developed a typical masculine ilio-sciatic notch, while on the left or normal side the notch was characteristically female. (c) It is not uncommon to find bones from opposite sides of the same pelvis unequally developed. One of the Predynastic Egyptian pelvises measured in the course of the present investigation gave a Chilotic Index of 109·3 for the right side (Fig. 6) and 92·7 for the left (Fig. 7). The Chorematic Index for the two sides was 6·3 and 18·1 respectively. An examination of the complete pelvis showed that the first piece of the sacrum, although normal on the right side was only partially sacralised on the left. The left hip-bone resembled the female type in being less heavily built, this being specially noticeable in the iliac crest, ischial tuberosity and body of ischium. Whether this striking asymmetry is due to lack of development of the left side of the sacrum, or whether the under-development of the whole left side of this pelvis, including the sacral anomaly, was brought about by feebler muscular development, as for instance in cases of paralysis while the bones are still growing, cannot be stated, but the fact remains that the more robust side developed as a normal male pelvis, while the weaker left has a majority of female characters. (d) Obstetricians not infrequently find that women of masculine build have difficulty in labour. This is in agreement with anatomical observation, where heavily built female pelvises are found to resemble the male type.

The results given above in the table of measurements for the women, show that the English women have the smallest pelves at least in the antero-posterior diameter. They are therefore less typically female than is the case in Egyptian women generally, and particularly so when compared with the women of the

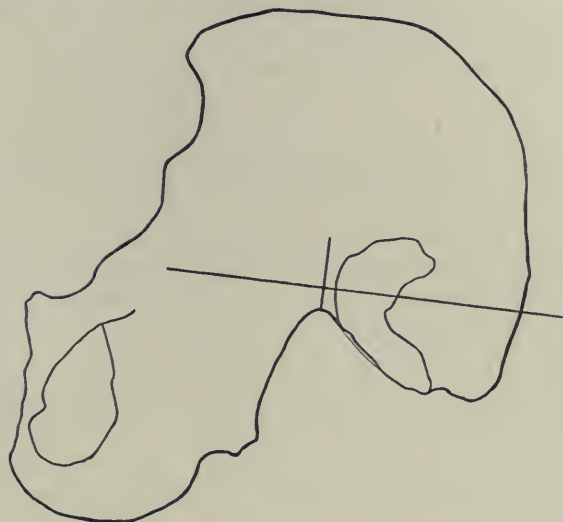


Fig. 6

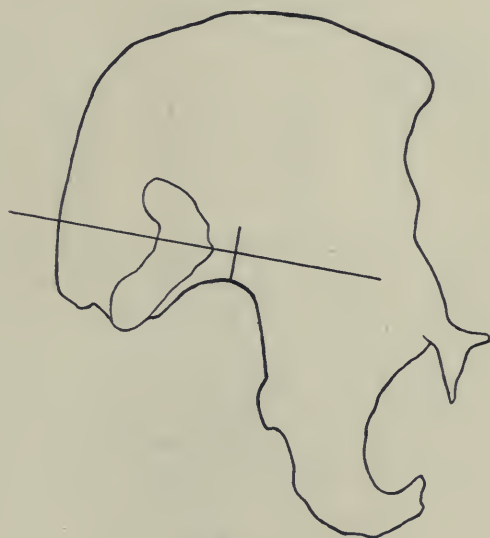


Fig. 7

VIIIth-XIIth Dynasties. A large antero-posterior diameter is of greater importance for an easy labour than a large transverse and the reduction of this in English women is possibly a cause of the difficulty in parturition which is so common an experience in England as compared with Egypt.



Now the evidence from the facts just adduced appears to point in the direction of weight as an important factor in the production of the male type of pelvis. This is certainly so in the case of the rickety pelvis. In the oblique pelvis instanced, the weight was unevenly distributed owing to the failure of development of one side of the sacrum, and the same may have been true in the pelvis exhibiting male and female characters on opposite sides, owing to the unequal development of the first piece of the sacrum. In the pelvis of a man with hydrocephalus described by the writer in this Journal, vol. XLVII, July, 1913, the left hip-bone in common with all the bones of the left side was under-developed owing to hemiplegia. Here again the ilio-seiatic notch was definitely wider on the left side, and the same bone exhibited a tendency to the formation of a pre-auricular sulcus, a female character. In this man the body weight was borne entirely on the right side, the pelvis was tilted to the left and the left ala of the sacrum was under-developed.

Although the facts adduced above seem to point to body weight as an important factor in the production of the different forms of the ilium in the two sexes, the evidence obtained from foetal bones measured in the same way is much less conclusive.

The following table gives the results of measurements made on four foetuses, two male and two female. All were full time with the exception of the second male in the annexed table, which was believed to be seven months when born.

Table III. *Foetuses*

Sex	Chilotie line		Total length	Chilotie Index	Pelvic Chilotie line		Chorematic Index
	Pelvic portion	Sacral portion			Antr. segment	Postr. segment	
Male	16.0	26.0	42.0	162.5	15.0	1.0	6.6
Male	13.5	17.5	31.0	129.6	13.0	0.5	3.8
Female	17.5	22.0	39.5	125.8	15.5	2.0	12.9
Female	18.0	21.5	39.5	119.4	16.0	2.0	12.5

While too much stress must not be laid on figures derived from such a small number of cases, it will be noticed that all the foetal hip-bones, irrespective of sex, yield the male type of *Chilotie Index*, but the two females are the lowest. In other words the characteristic difference, in the female, in the relation of the two portions of the Chilotie line, Pelvic and Sacral, though not pronounced at this early date is nevertheless suggested. At the same time the relation of the two segments of the Pelvic Chilotie line exhibited in the *Chorematic Index* also shows a definitely higher value in favour of the two females.

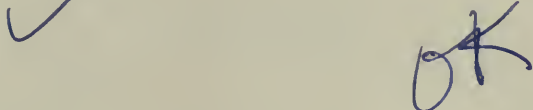
As there is no question here of the influence of the erect posture or of body weight, there must be an inherent tendency towards the formation of a sexual type, which as growth proceeds becomes more pronounced, from the influence of body weight, muscular development, and probably in the case of the woman, function, as represented by child-bearing.

In 1913 Dr Franz Weidenreich published in the *Anatomischer Anzeig.*, Nos.

20 and 21, the results of his investigations, "Über das Hüftbein und das Becken der Primaten und ihre Umformung durch den aufrechten gang." He approached the subject from a somewhat different point of view to that contained in this paper, as he was concerned with the measurement of the angles formed by the axes of the three constituent parts of the hip-bone, using the centre of the acetabulum as his point of departure. Nevertheless he reached substantially the same results in regard to the descent of the ilium in the higher apes and notably in man.

Although the figures dealt with in this communication refer only to the ilium, it is probable that an exhaustive series of measurements of the whole hip-bone would reveal a number of further points of value in determining the sex of a given individual. The work of Dr Weidenreich referred to above points strongly in this direction. But in order to do this satisfactorily it is necessary in the first place to increase the number of bones whose sex is definitely known.

Dr Aziz Girgis, Lecturer in Anatomy, and Dr B. Boulgakow, Curator of the Anatomical Museum, have rendered willing assistance in the photographing and preparation of the drawings, and grateful thanks are due to all those engaged in archaeological work in Egypt who have supplied the writer with material.



## A CASE OF DIVERTICULUM OF THE JEJUNUM

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DIVERTICULA of the jejunum appear to be extremely uncommon and perusal of the literature has brought to light only twenty-nine cases. This is perhaps remarkable, as the subject of diverticula of the intestinal tract has become of considerable interest, since the introduction of the opaque meal and radiography.

Fig. 1 shows a piece of jejunum which was removed at an autopsy from a male, of the age of 48, who died of cerebral thrombosis. At a point 18 inches from the duodeno-jejunal flexure, a diverticulum was found the size of the



Fig. 1

end of a finger. It protrudes from the jejunum along the mesenteric attachment. A small portion of it is under the mesentery, but the greater part is free. Vessels are spread out over its surface. The microscopic examination of its wall shows that it consists of all the layers found in the wall of a normal jejunum, muscle being present.

Another condition of interest was present in the abdomen. There was an infantile caecum lying just below the liver on the right side and the last 3 inches of the ileum had not a free mesenteric attachment, so these 3 inches of the small intestine were fixed to the posterior abdominal wall with no posterior covering of peritoneum (fig. 2).

Investigation of the recorded cases of jejunal diverticula shows the following facts.

(1) They are slightly more prevalent in the male sex.

(2) Two cases are reported in persons under the age of 20, but the majority are in persons over 50.



(3) Total cases of single diverticula, 11. Of these, 8 were within the mesentery, and 3 at the free border which had muscle in the wall.

(4) Total cases of multiple diverticula in the jejunum, 19, all within the mesentery. In 8 of these cases diverticula were found in other parts of the intestine, especially the duodenum.

(5) Many have not reported the number of diverticula present, but as many as 62 are reported in the jejunum in one case.

(6) Pancreatic tissue was found at the end of one diverticulum.

(7) One observer suggests that a diverticulum 2 feet from the pylorus, which had a mesentery was a Meckel's diverticulum. In view of the report(1) on the position of this structure, this seems improbable.

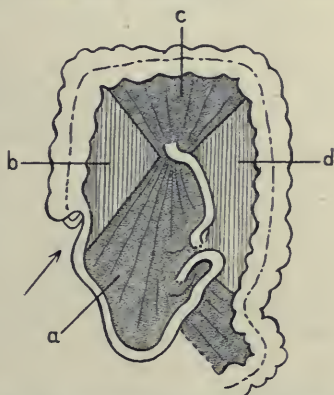


Fig. 2. Diagram to illustrate obliteration of mesentery of terminal 3 inches of ileum.

*a*, the mesentery; *b*, mesentery obliterated; *c*, transverse mesocolon; *d*, descending mesocolon obliterated.

#### FORMATION OF DIVERTICULA

The persistence of a Meckel's diverticulum is well recognised and being a remnant of intrauterine life, where its presence is a necessity, it must be placed in a separate category to the other diverticula of the intestinal tract.

The other diverticula of the large and small gut are usually regarded as pathological in origin. The theory put forward to explain their origin being that along the mesenteric border there is a weak area in the intestinal wall, owing to the penetration of the blood vessels. This will explain the jejunum being less subject to diverticula, owing to its possessing thicker walls and a larger lumen.

However, the embryological work of Lewis and Thyng(2) is of interest as their deduction is that the majority of the diverticula are of congenital origin. They studied sections of the embryo of pig, rabbit and man, and of the cat and sheep. In the embryos of the first three, they found the regular occurrence of knob-like diverticula, and they were often present in the cat and sheep. They were also noted along the bile and cystic ducts. In older embryos they are more numerous, especially in the distal part of the small intestine. None were found in the large intestine except near the ileocaecal valve.

They suggest that possibly these knob-like projections give rise to so-called pathological diverticula.

This work was done some 15 years ago, but I cannot find any confirmation of the findings.

I am indebted to Miss Pickering for the two diagrams.

#### *Analysis of recorded cases*

The following is a list of the cases that are reported and the more important facts relating to each case are briefly noted.

# Jejunal Diverticula.

Case	Type		Attachment		Sex	Age	Other intestinal abnormalities	Remarks	Reported by
	Single	Multiple	At free border of jejunum	Within the mesentery					
1	x	—	x	partly	M	48	Infantile caecum	No mesentery to the last 3 ins. of ileum. P.M. specimen	Buxton
2	x	—	—	x	F	30	—	In middle of the jejunum. P.M. specimen	Cornillon (3)
3	x	—	—	x	M	77	—	3 ft. from duodeno-jejunal flexure. ? Meckel's diverticulum. P.M. specimen	Buzzi (4)
4	x	—	—	x	M	6	—	Very large and caused intestinal obstruction	Buchwald (5)
5	x	—	x	—	M	14	—	Pancreatic tissue at the end of the diverticulum. P.M. specimen	Hansemann (6)
6	x	—	—	x	?	?	—	Museum specimen	Fischer (7)
7	x	—	—	x	F	50	—	Below opening of common duct. P.M. specimen	Latarjet (8)
8	x	—	—	?	M	54	—	Operation case	Hunt (9)
9	x	—	—	x	M	44	—	P.M. specimen	Hunt (9)
10	x	—	x	—	M	75	—	2 ft. from pylorus. Had a mesentery. ? Meckel's diverticulum. P.M. specimen	Clarkson and Collard (10)
11	x	—	—	x	M	61	—	4 ins. from duodeno-jejunal flexure. Museum specimen	Clarkson and Collard (10)
12	—	5	—	x	F	59	—	Operation case	Terry (11)
13	—	x	—	x	M	50	—	P.M. specimen	Cooper (12)
14	—	53	—	x	M	65	—		Osler (13)
15	—	3	—	x	M	40	Congenital stricture of jejunum at the duodeno-jejunal flexure	Large "diverticula. Walls had all the intestinal coats. No symptoms and patient died of bronchitis	Moore (14)
16	—	x	—	x	M	old	Diverticula in ileum also	All herniae through muscularis mucosa. P.M. specimen	Virchow (15)
17	—	7	—	x	F	73	—	P.M. specimen	Edel (16)
18	—	x	—	x	?	?	—	"	Seippel (17)
19	—	x	—	x	M	85	—	"	Hansemann (6)
20	—	x	—	x	M	73	Diverticula in stomach, duodenum and colon	Died of perf. duodenal ulcer. Many diverticula in the jejunum and 13 the size of a walnut, all herniae through muscularis mucosa	Grassberger (18)
21	—	50	—	x	F	50	—	All herniae through muscularis mucosa	Nicholls (19)
22	—	x	—	x	F	68	Also in colon	P.M. specimen	Latarjet (8)
23	—	62	—	x	M	45	Two in duodenum	"	Braithwaite (20)
24	—	12	—	x	M	61	—	Operation case	Case (21)
25	—	30	—	x	M	73	Also in ileum and pelvic colon	"	Case (21)
26	—	x	—	x	F	43	Also in duodenum	Operation case. Herniae through muscularis mucosa	MacKechnie (22)
27	—	7	—	x	M	71	—	P.M. specimen	McWilliams (23)
28	—	x	—	x	F	45	13 in lower jejunum and upper ileum	Operation case. Herniae through muscularis mucosa	Gordinier (24)
29	—	4	—	x	—	—	—	Operation case. All at beginning of jejunum	Balfour (25)
30	—	6	—	x	F	77	One in duodenum	P.M. specimen. Herniae through muscularis mucosa	Good (26)

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## REVIEW

*The Physiology of Twinning.* By HORATIO HACKETT NEWMAN, Professor of Zoology, University of Chicago. Pp. 230 + xii, figs. 71. (Chicago University Press), 1922. Price 1.75 dollars.

Human anatomists are more interested in the imperfect formation of twins than in their perfect production, but whether their interest lies in the one form or in the other we commend to them this convenient treatise by Professor Newman. "For a long time," says the author, "I have held the view that twinning is essentially a phenomenon involving a physiological isolation of equivalent parts of the blastoderm and a regulation of the isolated or twinned regions into complete embryos. As to the cause of physiological isolation I have maintained, for the armadillo at least, that the essential feature is temporary cessation or radical retardation of development at a critical period."

The author bases his explanation of twin-production on a theory which has been nursed and extended by American biologists in recent years—the theory that there exists "gradients of vitality" in all living masses. In another form the theory is familiar to students of living pulsating non-striated muscle—who regard the pace-making centres of the heart as dominating the rhythm of the whole mass—because the leading nodal centre is endowed with the greatest vitality. The embryologist presumes that the blastoderm has a dominating centre; twinning follows if this single centre becomes duplicated. The essential theory of dominance is very fully discussed in another volume of the Chicago University series by Prof. Charles M. Child, entitled *The Origin and Development of the Nervous System from a Physiological Point of View*.

A. K.

## VITAL STAINING OF THE LEPTOMENINGES

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IN 1913 Goldmann<sup>(6)</sup> published an account of his experiments with vital dyes injected into the subarachnoid space of rabbits and dogs. The subarachnoid space was reached by trepanation of the skull or by laminectomy of the vertebral column. In rabbits the dose used was 0.5 c.c. of a 0.5 per cent. solution of trypan blue, while in dogs, 2 to 2.5 c.c. of a 1 per cent. solution were given. The immediate reaction of the animals demonstrated an extreme toxicity of the injected substances, for muscular spasm, tonic and clonic contractions, acceleration of respiration and heart-beat, then coma, and death of the animal in about nine hours followed. The author drew attention to the heightened toxicity of foreign substances when introduced by way of the cerebrospinal fluid and mentioned various observers who had demonstrated the increased toxicity of such substances as morphia, cocaine, potassium ferrocyanide, methylene blue and ferrocyanates when injected in the subarachnoid space.

Taking the most favourable of these experiments (those in which the animals survived the longest period after the injection), Goldmann made the following observations: The surface of the spinal cord was stained to a depth of 2 mm. throughout its whole extent, and the dye could be followed out around the spinal ganglia. The cerebral hemispheres exhibited a coloration similar to that of the spinal cord, but the stain was of a lighter hue. The blue was especially deep at the base of the brain and passed outward along the optic nerves to the corneo-scleral junction and along the olfactory nerves to the nasal cavities. The convexity of the brain was uncoloured, and only along the larger vessels could blue stripes be seen. The stain invaded the ventricles of the brain and the central canal of the spinal cord. Outside the central nervous system the trypan blue was seen in the sheaths of the large blood-vessels and in the liver and kidney. These findings occurred without exception in animals which exhibited the toxic symptoms described above.

Microscopically, Goldmann found the leptomeninges to be stained a diffuse blue. The pial blood vessels entering the brain substance were coloured, as were the nuclei and network of the glial cells. The ganglion cells of the anterior and posterior horns always showed a deposit of stain in the nucleus and their processes were distinctly outlined by the dye. The glial and pyramidal cells of the cerebral cortex and the Purkinje cells of the cerebellum were customarily

coloured with blue. When weak doses were used the ganglion cells appeared free from dye, but even in these cases, when observed with the oil immersion lens, fine blue granules could be found in the cells of the anterior and posterior horns. This coloration was not diffuse and the nucleus was unstained; Goldmann therefore concluded that they were not moribund cells. The pial septa were everywhere coloured and the cells lining the perivascular spaces showed blue granules. The cells in the arachnoid and pia bearing the stain and those extending from these membranes into the brain he regarded as similar to the so-called "pyrrhol" cells of the liver and spleen and connective tissues.

Goldmann's experiments seemed, on critical analysis, to be complicated by the toxicity of the dye in the dosage used for subarachnoid injection. This intraspinal toxicity was indicated by the reactions of the animals to such administration of the dye-stuff and by the more or less diffuse staining of the cellular elements of the nervous tissue itself. The present report is based on a series of experiments, which though similar to those of Goldmann have been planned with the object of avoiding the obvious limitations of his earlier work, and they have afforded definite information regarding the cell-morphology in the subarachnoid space.

#### VITAL STAINING UNDER NORMAL CONDITIONS

The animals chosen for the work were cats; the route of injection into the subarachnoid space was by an occipito-atlantal puncture into the cisterna magna (cerebello-medullaris). The dye used was trypan blue and the strength found most satisfactory was a 0.1 per cent. solution. The dye was first made up in a 1 per cent. aqueous solution; this was diluted with Ringer's solution to the desired strength. The procedure followed consisted of etherization of the animal, sterilization of the chosen area and puncture into the subarachnoid space with a suitable lumbar puncture needle. After release of the cerebrospinal fluid, a syringe containing the selected amount of dye (6 to 8 c.c.) was attached to the needle and the solution slowly injected. When 6 c.c. had been injected, the animal frequently exhibited a tonic spasm, with extension of the limbs, arching of the back, and extension of the head. This phenomenon, apparently due to increase in intracranial tension, passed off in a few minutes, and after recovery from the ether anaesthetic, the cat behaved normally. The injections were repeated on alternate days; between the injections the animals ate well, cleansed themselves and were active and normal in every respect. The cerebrospinal fluid removed was examined on each occasion but with the experimental procedure carried out as outlined no cells were ever found in it. As was mentioned a 0.1 per cent. solution of the dye was found to be the most satisfactory, for with this dosage the cats were perfectly normal in the intervals. If a 0.2 per cent. solution was used the dose was fairly well borne, but between the doses the cats were lethargic. If a 0.3 per cent. solution was given, the cats, though they exhibited no muscular phenomena, were torpid, ate little and did not cleanse themselves.



The following protocols give a summary of the cats stained according to the above procedure:

*Cat 1.* This cat was given, in three injections, 15 c.c. of a 0.1 per cent. solution of trypan blue in Ringer's solution. The cerebrospinal fluid, removed before each injection, contained no cells. The cat remained in good condition and was killed 48 hours after the last injection of the dye and fixed in 10 per cent. formalin by aortic injection.

*Cat 2.* This cat received 22 c.c. of a 0.1 per cent. trypan blue solution. The initial dose given in this case was 10 c.c. After this injection the animal became lethargic. Two subsequent injections of 6 c.c. were given. As the animal was becoming weaker it was killed and injected as above.

*Cat 3.* This cat received, in seven injections, 42 c.c. of the 0.1 per cent. trypan blue solution. The cerebrospinal fluid remained free from cells. The cat was perfectly well during the intervals and was killed and fixed in 10 per cent. formalin 48 hours after the last injection.

*Cat 4.* This cat received, in eight injections of 8 c.c. each, 64 c.c. of the 0.1 per cent. trypan blue. The animal remained in excellent condition throughout the experiment and the cerebrospinal fluid was always free from cells. The animal was killed, fixed in 10 per cent. formalin by aortic injection eight hours after the last injection of trypan blue.

*Cat 5.* The dye received by this animal had salted out before it was injected and after a dose of 6 c.c., the animal exhibited convulsive movements. The spasms came on five minutes after the cessation of the injection; coma soon supervened and death followed quickly. Examination showed everywhere an indiscriminate staining of meninges and nerve cells indicating the well-established manner of staining of injured or dead tissues.

**MACROSCOPIC EXAMINATION.** After fixation of the animal by injection through the heart with 10 per cent. formalin, the skull and vertebral column were detached from the rest of the body and the vertebral arches were opened; this block of tissue was placed in 10 per cent. formalin for three or four days for further fixation. At the end of this time the central nervous system with membranes intact was detached completely from the bone.

The whole surface of the central nervous system and membranes appeared intensely blue. The only unstained structures were the spinal ganglia and the pituitary gland. On closer examination of the spinal nerves, the anterior and posterior roots appeared as white strands clothed in blue membranes which ceased on the proximal side of the ganglia. The cranial nerves passed out through the cranial foramina as white strands. The Gasserian ganglia were perfectly white. The superficies of the optic nerve and chiasma were blue and the investing blue membrane reached the posterior pole of the eyeball. The olfactory bulb was enveloped in blue but the stain did not accompany the olfactory fila and no stain appeared in the olfactory mucous membrane. The intensity of stain was more marked in the area adjacent to the site of the injection. In those animals which were lightly stained the dye was most

marked over the cervical cord, base of the brain, cerebellum and occipital poles of the cerebrum. In those more heavily stained, the coloration attained a more uniform intensity, the convexity of the cerebral hemispheres, as well as the caudal end of the spinal cord, showing the same intensity as around the site of injection. When the dura was raised up it was pale and semi-transparent and quite free from the dye. The membranes underlying the dura were intensely blue. Transverse sections of the spinal cord showed a faint blue stain which appeared to be confined to the white matter of the cord. The blue colour faded out before the grey matter was reached and the latter appeared entirely unstained. Cross sections of the brain and cerebellum showed a faint blue coloration of the cortex extending inward from the pia. The ependymal lining of the ventricular system was free from the dye and the choroid plexuses were pale and unstained. The dura in the hypophysial region when lifted away disclosed the pale pituitary body embraced circumferentially around its attachment to the brain by the blue coloured arachnoid.

At the site of injection there was always a slight leakage of trypan blue into the adjacent extradural tissues. Lymphatics could be traced to the large vitally stained lymphatic glands at the base of the skull. These glands bore a considerable amount of dye but the dye had apparently reached them from the site of extravasation and not from their cranial connections. In the more lightly stained animals these glands were only slightly coloured. The liver, spleen and kidney, showed no signs of visible coloration in any of the animals.

These observations stand in marked contrast to the failure of the central nervous system to stain when the vital dye reaches it through the blood stream. For after intravascular injection in a healthy animal only the dura and the choroid plexuses are deeply stained, though the pituitary and the adjacent tuber cinereum are faintly coloured (Goldmann). Further, Wislocki and Putnam (16) found that the small *areae postremae* (areas rich in blood-vessels and glial tissue) of the fourth ventricle were coloured by the dye. None of these areas took up the stain from the subarachnoid space. Furthermore, the leptomeninges on vital staining through the blood stream are uncoloured, whereas on subarachnoid injection these membranes are intensely stained. The faint bluish coloration of the peripheral zones of the nervous tissues on subarachnoid injection of the vital dye is also to be contrasted with the lack of staining of these zones after intravascular injection of the trypan blue.

**MICROSCOPIC EXAMINATION.** With the aid of the binocular microscope the membranes were dissected off the cord and the brain. The dura mater from all regions of the brain and spinal cord was entirely free from any evidence of staining with trypan blue. The arachnoid was carefully raised from the pia and the numerous delicate trabeculae uniting the arachnoid to the pia were divided with finely pointed scissors. The membranes were counterstained in carmine and mounted as films, care being taken in the case of the arachnoid to have the subdural surface next to the slide. The blue colour of the arachnoid enabled one, in dissecting it away from the pia, to see that it did not enter any of the



fissures of the cord and that it embraced the anterior and dorsal nerve roots ceasing proximally to the spinal ganglia on the dorsal root and at an equivalent position on the ventral roots.

The histology of the arachnoid and pia has been described by Weed (14) as follows (p. 398):

"The arachnoid is a cellular structure with a delicate supporting reticulum of white fibrous and yellow elastic fibrils, covered on both sides by characteristic flat cells. From the inner side of this membrane project small, easily-broken trabeculae, upon which are contained the cells forming the inner lining of the arachnoidea. The core of such an arachnoid trabecula is composed of a few connective tissue fibrils, united on the outside with the fibrous framework of the membrane and on the inner side with the sub-pial tissues...."

"The pia mater,...closely invests the nervous system, continuing into the cerebral sulci and into the medial fissures of the cord. Actually...it is essentially constituted by the 'visceral' reflection of the cells of the arachnoidea, but it possesses in addition an underlying supporting structure of a few connective tissue fibrils and neuroglial elements."..."Quite similarly, all of these vessels perforating the fluid-spaces between pia and arachnoid are likewise covered by an inclosing investment of mesothelial cells. Thus, the sub-arachnoid space (or, better, spaces) become a fluid-bed, everywhere lined by the typical, very low mesothelial cell."

The essential structures mentioned in this description were adequately demonstrated in the spread preparations of the leptomeninges of these vitally stained animals, but other elements in the arachnoid should be mentioned. These are the arachnoid clusters or whorls of flattened cells which may be confined to the arachnoid or may hypertrophy and penetrate the dura, and secondly the arachnoid villi—projections of the arachnoid, covered by a layer of mesothelium—into the walls of the great sinuses. Both of these structures have been recently described by Weed (13,15).

In the preparations of the leptomeninges three orders of cells taking up the dye could be distinguished in the arachnoid and pia. The first was the clasmato-cyte. In the cytoplasm of these cells the dye was accumulated in granules of various size and depth of colour. The dye had the appearance of being stored in vacuoles ("segregation vacuoles," Shipley (12)). Other features, such as the well-defined nuclear membrane, the scanty chromatin, the eccentric position of the nucleus, the presence of a concavity in the nucleus towards the main protoplasmic mass were all present. The shape and size of the cells varied somewhat but they were usually round or oval and slightly larger than a polymorphonuclear leucocyte.

The second cell that could be distinguished by the presence of granules of trypan blue in its cytoplasm was the mesothelial lining cell. These could be seen to best advantage on the trabeculae. Elongated, flattened out, with rod-like nucleus and scanty cytoplasm, they were characterized by the presence of a few granules of the dye. These granules were very tiny and discrete.



They were sparse in number and close together in the cytoplasm, near to either pole of the nucleus. The dye was confined to these two areas and did not extend into the remainder of the cell.

When the films of animals which had been more heavily stained were studied, the type of aggregation of the dye-granules within these mesothelial cells was noted to be somewhat different from that in the animals which had received smaller amounts of stain. Furthermore, in these animals cell multiplication had taken place. Though mitotic figures were more easily found in the cells on the trabeculae, yet the same process could be made out in the flattened areas between the origin of the trabeculae. Secondly, many of the mesothelial cells appeared to be rounding up and acquiring a cuboidal form, with the round, palely staining nucleus occupying the centre of an increased amount of cytoplasm which was studded with fine granules of blue. In presumably older cells, which were still lying spread on the trabeculae or so far rounded up that their attachment to the trabeculae had become quite attenuated, the nucleus had become eccentric and was concave toward the part of the cell where the cytoplasm had accumulated. In this intracellular area the trypan blue was not accumulated and the granules were coarser though not so large as those contained in the elasmatocytes. Further small vacuoles were distinguishable.

Thus under the influence of the irritation of the dye there had been induced in the mesothelial cell a series of changes of which the final result was to produce a mononuclear phagocytic cell of a morphology somewhat similar to that of the elasmatocyte, yet distinguishable by the smaller amount of the dye by less coarse clumping of the blue granules, and by the fewer and rarer vacuoles.

The third cell containing granules was the fibroblast. A pale round nucleus with a narrow ring of cytoplasm and many branching processes characterized this cell which took up the dye in a notable way. Around the nucleus in the ring of protoplasm a perinuclear ring of fine discrete granules of dye could be seen and the same type of fine discrete granules was noted in the processes of the cells. No perceptible changes in the form of the fibroblast were encountered on comparing the films from lightly or more heavily stained animals. Fibroblasts were found to be relatively few in the leptomeninges.

In the villi and arachnoidal cell-clusters occasional mononuclear phagocytic cells containing aggregations of dye were seen but the main mass of cells making up these structures was free from trypan blue. In a cell-cluster of the arachnoid which had hypertrophied and advanced towards the dura an occasional dye-bearing cell beyond the level of the dural surface of the arachnoid was visible. The dura never contained any dye-bearing cells and the presence of vital dye in these cell clusters bears out the arachnoidal origin of these dural cell-inclusions.

In the pia the same analysis of the cells held good. The endothelium of the blood-vessels contained none of the dye. The dye accompanied the pial tissue for a short distance into the choroid plexuses but none reached the choroidal

epithelial cells. In the region of the pituitary, the dye was present in the arachnoid on the anterior surface of the gland. Though a continuation of the subarachnoid space (Hughson (5)) has been shown, by the injection of potassium ferrocyanide and iron ammonium citrate under certain experimental conditions, to encircle the pituitary, yet with trypan blue, the dye was not found about the base of the gland.

As is fairly well established, the perivascular spaces which surround the entering vessels of the spinal cord and brain are lined by mesothelial cells of the pia which continue inward for a certain distance. In the spinal cord of the specimens of the present series, flattened mesothelial cells bearing fine discrete granules of dye in the cytoplasm at either nuclear pole could be traced inward along the entering vessels. In some instances they could be followed across the white matter and still in continuity with the perivascular space could be found in the grey matter of the cord. In the cortex a similar phenomenon was visible. Along an entering vessel these mesothelial cells bearing granules of dye could be traced and could be found for a short distance along the lateral branches of the vessels, if these were comparatively large. However, they were not found to line the whole space, for the cells with blue granules were limited to the more peripheral portions of the perivascular channels; in general, however, they continued to the smaller arterioles and venules before ceasing to line the perivascular cuff. In the perineuronal space and about the capillaries there were no dye-bearing cells and here the lining cells appeared to be neuroglial.

The epidermal cells—nerve cells, ependymal cells, and neuroglial cells—in no instance contained the vital dye when administered by the subarachnoid route. Blocks of nerve tissue were sectioned in celloidin and carefully examined but the nerve cells were never found to contain dye. The ventricular lining, the cells of the central canal, and the medullary vela were free from stain. Under pathological conditions (MacCurdy and Evans (9), infantile palsy; Macklin (7), MacCurdy (10), Mertzbacher (11), Essick (4), with experimental inflammation), vital staining of nerve cells and neuroglia occurs after intravascular injection, but under these conditions the cells are dead or damaged.

Thus it seems logical to conclude that when a vital dye, such as trypan blue, is injected into subarachnoid space it remains confined to the membranes which bound that space: the dye is taken up in great quantities by the mesothelial lining cells, by the clasmatocytes, and to a slight extent by the fibroblasts. The presence of dye-bearing cells determines accurately the limits of the mesodermal leptomeninges and thus it becomes possible to establish the pial boundaries of the perivascular spaces of the central nervous system and to substantiate the arachnoidal origin of the cell-inclusions in the dura.

#### VITAL STAINING UNDER CONDITIONS OF IRRITATION

It was believed that if such a vitally stained animal were subjected to further irritation of the leptomeninges so that free cells occurred in the cerebro-





Films of the leptomeninges prepared from the first of these animals showed, that, as Essick had found, the initial reaction to the laked corpuscles was the pouring into the cerebrospinal fluid of a great number of polymorphonuclear leucocytes. At 18 hours after the injection the polymorphonuclears were greatly in excess, mononuclear phagocytic cells being relatively few. (The film showed numerous red corpuscles derived from the injection.) The films made 24 hours after injection showed a great increase in the number of mononuclear phagocytic cells. Many polymorphonuclears and injected corpuscles were still present. Some films were made on slides that had been prepared with a layer of neutral red according to the method used by Dr Sabin (verbal communication); two kinds of mononuclear phagocytic cells were distinguished. The larger kind seemed to be a typical clasmatocyte with irregular cell outline, with granular protoplasm, vacuoles, and containing neutral red granules and fragmented or entire red corpuscles. The other mononuclear phagocytic cells were smaller in size, more round in outline; the granules of neutral red taken up were much finer and vacuoles were not obvious. This differentiation of the mononuclear cells into two types was not apparent in films prepared from this animal 40 hours after the injection of laked blood. While the polymorphonuclear cells were few in number, the mononuclear elements were also very scarce and were all of the clasmatocyte type.

The animal was then killed and fixed by injection of 10 per cent. formalin through the heart. The specimen of the nervous system showed relatively slight coloration with the blue. Spread preparations of the arachnoid and pia were stained and mounted as before. The same cellular pictures described for the vital dye films were again identified. Many polymorphonuclears were seen on the spreads and red corpuscles, still uningested, were present. The trabeculae showed most clearly the changes which had occurred. Cell division was abundant. Cells rounding up, becoming plumper and disengaging themselves from the trabeculae could be seen. These cells before disengaging themselves seemed to have undergone division because wherever a cell seemed to be nearly free a small cell with its nucleus opposite that of the pedunculated cell was apparent. In this way the trabeculae were not denuded of cells. These disengaging cells had concentrated their vital dye towards the major protoplasmic mass and the nucleus had become eccentric. Fragments of red corpuscles and vacuoles lined with blue were apparent in them.

These findings confirm the results of Essick. The use of trypan blue though not of determining value in this case as a criterion of cell-type among the free mononuclear cells of the cerebrospinal fluid did afford preparations which suggested strongly that the mesothelial cell as it became transformed into a free mononuclear phagocytic cell resembled in certain particulars the clasmatocyte, two essential points of difference remaining. The mononuclear phagocytic cell derived from mesothelial cells of the leptomeninges was smaller and the granules of dye, whether neutral red or trypan blue, were finer than in the true clasmatocyte. The maintenance of these differences permits the assump-

tion that the cells are genetically separate and that they do not, under the conditions of observations, become identical.

Cats 2 and 3 were heavily stained and the films of cerebrospinal fluid displayed polymorphonuclear leucocytes and mononuclear phagocytic cells of the clasmatocyte type. Study of warm box preparations and stained films did not enable one to distinguish varieties in the mononuclear phagocytic cells. A few mononuclear cells without any trypan blue granules were encountered—perhaps desquamated mesothelial cells. The clasmatocytes free in the cerebrospinal fluid were heavily stained with trypan blue. On examining the membranes there could be no doubt that lining cells were rounding up and engulfing red blood corpuscles and polymorphonuclears; the dye was in fairly large granular masses and vacuoles were present. Some of these cells were quite round; others, spindle shaped, with their poles prolonged into fine processes; others were slender and elongated. They were superficial to the clasmatocytes, which could be identified at a deeper level in the spread-preparation.

It was hardly possible to distinguish varieties in the mononuclear phagocytic cells in the cerebrospinal fluid and almost equally difficult in the films of the fluid, but here in the spread-preparations the difference in position assured one of the separate identity of lining cells and clasmatocytes. Mesothelial lining cells whose transformation to mononuclear phagocytic cells was complete lay in continuity with less advanced cells and formed the surface of the preparation. Beneath this layer true clasmatocytes could be brought into focus.

#### DISCUSSION

Mallory (8) has suggested that the mesothelial lining cell of the subarachnoid space is a flattened out fibroblast. The fibroblast in these spread preparations behaved in the characteristic fashion toward trypan blue, determined by many investigators; no evidence was found of this highly differentiated cell becoming a free mononuclear phagocytic cell in the cerebrospinal fluid. The mesothelial covering cell of the leptomeninges presented a reaction to trypan blue which was characteristic. First a few fine granules appeared in the cytoplasm at either pole of the nucleus. Then as the dye, on further injections, increased in amount, these cells underwent division, rounded up and showed many more fine granules of dye in their cytoplasm and in the most extreme case (Cat 5), many cells still lying on the trabeculae showed an eccentric nucleus, and accumulation of dye in the major portion of the cytoplasm, and vacuoles. Furthermore, they ingested laked blood corpuscles, fragments or whole polymorphonuclears and became in certain respects indistinguishable from a clasmatocyte. Whether they became free in the cerebrospinal fluid or not, these experiments have not conclusively determined.

In a study of the serosal cells of the peritoneum, Cunningham found that these cells did not contribute to the mononuclear phagocytic cells of peritoneal exudates. His review of the literature shows how difficult it is to interpret the

evidence and this study necessarily suffers from the same defect. It appears, however, that the mesothelial cell of the subarachnoid space is not identical with the serosal cell of the serous-cavities but is a less differentiated cell, somewhat more primitive in type, capable of becoming under sufficient stimulation a mononuclear phagocytic cell.

Other studies on the inflammation of the brain and subarachnoid space (Macklin (7), MacCurdy (10), Ayer (1), Essick (4), and Mertzbacher (11)) have given the mesodermal elements of the pia and arachnoid as the chief source of the mononuclear phagocytic cells. Mertzbacher indeed included the neuroglia, the lymphocytes of the blood and the endothelium of capillaries amongst the sources of his "Abraumzellen." Yet an analysis of the above shows the elements of the pia-arachnoid as the chief source. Our studies indicate that the mesodermal elements of the pia and arachnoid capable of becoming mononuclear phagocytic cells, are not only the clasmatoocytes but also the mesothelial lining cells; though we did not succeed in obtaining conclusive demonstration of the presence of the second group free in the cerebrospinal fluid, yet the finding of two clearly defined types of mononuclear phagocytic cells in the preparations and films of the fluid, in addition to the evidence of reaction of these cells while still attached to the membrane, leads us to believe that the lining cells of the subarachnoid space form such free mononuclear phagocytic cells in the cerebrospinal fluid.

#### SUMMARY

1. The injection of vital dye into the subarachnoid space outlines the confines of that space, demonstrating the mesothelial lining cell completely enclosing the fluid-channels and continuing inward in the perivascular channels.
2. The dye is ingested by the lining mesothelial cells, by clasmatoocytes, and by fibroblasts.
3. Under the influence of the dye and of partially destroyed red blood corpuscles, the lining cells become transformed into vacuolated, mononuclear, phagocytic cells.
4. The free mononuclear phagocytic cells of the cerebrospinal fluid under these conditions are derived from clasmatoocytes and also in all probability from the mesothelial lining cells.

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# ON THE APPLICATION OF THE SPALTEHOLTZ CLEARING METHOD TO THE STUDY OF THICK SERIAL SECTIONS OF EMBRYOS, WITH DEMONSTRATION OF SPECIMENS

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THE Spalteholtz method of producing transparent anatomical preparations is now well known and widely practised. Originally introduced as a macroscopic method it has been extensively employed, especially in America, in the study of embryonic structure, and more particularly in the clearing, *in toto*, of injected embryos or considerable parts of them. It has also been extensively used in the clearing of embryos whose cartilaginous skeletons have been previously stained by the Van Wijhe method.

At the summer meeting of the Society last year I showed a number of preparations to illustrate the application of the same method to series of quite thick sections of embryos. Since then I have prepared a number of additional serial preparations, several of which I am exhibiting at this meeting. I have found the results of the experiment so instructive that I venture once more to call the attention of the Society to the method as an extremely useful adjunct to microscopical investigation by means of serial sections of the usual type.

Whilst there is nothing really novel in the procedure itself, I have not been able to discover any record of precisely the same application of the method in embryological study. In the systematic study of embryonic structure by means of serial sections it has hitherto been our aim, usually, if not invariably, to obtain complete series of quite thin sections. This is, of course, indispensable for the study of cytological or any minute structural detail; but much embryological work is concerned, not with the most minute structural detail, but with grosser morphological features in the shape of cell-groups, tissue-masses and rudiments of developing organs whose form and relations can be more readily apprehended if studied in thickish blocks than in very thin sections. This the Spalteholtz method enables us to do very simply and conveniently, as I think my demonstration specimens will show.

A 12 mm. embryo cut in transverse series in the usual way into sections of, say, 10 micra thick will involve the study of some twelve hundred sections, each of which furnishes an image of structure practically in two dimensions only. To obtain from such a series anything like a vivid stereognostic conception of structure requires a considerable effort in the way of mental reconstruction and indeed often demands actual graphic reconstruction by diagrams or models. I claim that much of this difficulty is obviated, so far as

the larger features of structure are concerned, by the study of thick serial sectional blocks treated by the Spalteholz method.

I call your attention, for example, to one of my demonstration specimens in which the entire system of bronchial buds in the lung of a mammalian embryo may be directly seen under the binocular microscope as clearly and stereoscopically as if they were represented in a wax plate model. Although the method I employ cannot in any full sense be called a new one it is perhaps desirable to set forth the small expedients by which such a series is prepared.

Let us suppose there is a 12 mm. mammalian embryo to be studied in transverse series by this method. It is first of all infiltrated with celloidin and a good celloidin block made of it in the usual way. This block is then trimmed into rectangular form, keeping fairly near, though not too close, to the embryo. The elongated block thus obtained has now to be cut into transverse serial sections. Before doing so it is good to cut off obliquely one of the four longitudinal margins of the block so that each cross section will show a cut-off corner for orientation purposes.

I usually cut the sections at anything from .5 to 1 mm. in thickness, preferably about .5 mm. The sections may be cut after mounting the block on any microtome which will allow of elevation of the knife for the necessary distance between the sections; but I have cut practically all my sections free hand, laying the celloidin block on a sheet of cork and cutting vertically with a Gillette razor blade held in the hand. I use a pair of magnifying spectacles during the operation. Such free hand operations, of course, involve some irregularity, both in thickness and in plane, but it is not necessary to have the sections of equal thickness and there is sometimes a certain advantage in varying both the thickness and the plane. Thus, for example, with a curved embryo one can often with advantage cut somewhat wedge-shaped slices. Their structural relations can quite easily be correctly interpreted when they are mounted. A 12 mm. embryo will yield, say, 24 half-millimetre sections.

As each section is cut it is transferred to a capsule of alcohol or water. Commonly a dozen capsules will suffice in the case of an object of this size, for it is usually easy to distinguish the second cycle of sections from the first. But, of course, any other expedient for keeping the serial sections in their proper order may be adopted.

During cutting, the block must not be allowed to get dry. After cutting, the sections are transferred to distilled water, if they have not been placed directly in it; or they may be transferred directly to the staining fluid utilizing the same capsules. The staining of the blocks is of the utmost importance. The secret of the method, indeed, is the attainment of an adequate but very light and transparent stain. I have obtained the best results with a very weak haematoxylin stain.

I usually stain in a fluid consisting of 5 per cent. ammonia-alum solution, to which has been added enough haematoxylin stain to give a claret-and-water colour. In this the sections remain all night. It is sometimes advantageous to differentiate for a few hours in pure ammonia-alum solution, 5 per cent. The



sections are then transferred to distilled water in which it is necessary to wash out the alum thoroughly otherwise crystals form during de-hydration. At this stage, of distilled water, they are now to be fixed on a microscope slide. A 10 to 20 per cent. solution of clear gelatin is prepared, to 50 c.c. of which a few drops of absolute phenol are added. I keep a stock of this in a wide test tube and heat it up as required in a beaker of water. A layer of the gelatin is poured on an ordinary microscope slide and with a fine forceps the celloidin sectional blocks are, as quickly as possible, placed in the warm fluid gelatin layer arranged in their proper serial order. The obliquely-cut corner of each section permits of this being done readily and in correct orientation.

In order to avoid premature setting of the gelatin before the manipulation is completed it is well to carry on the operation on a temporary warm stage formed by a glass plate placed over a beaker of hot water. During the operation it is well to affix a descriptive label on the slide in the gelatin of the mount. When the sections are in position the gelatin is allowed to set. Care must be taken prior to setting to get rid of any air bubbles that may form. The setting of the gelatin should be accelerated by placing the slide on a cold surface. Setting should occur before the surfaces of the sections become dry, but if there is any tendency to desiccation of the sections they must be kept moist with a wetted camel hair brush.

When the slide is set it should be placed carefully in formalin solution, 5 or 10 per cent., care being taken to liberate any bubbles that may tend to form. The slide may then be passed through ascending alcohols into absolute, then cleared in benzol and finally transferred to one of the Spalteholz fluids.

For embryonic tissues I use three parts of artificial oil of wintergreen to one part of benzyl benzoate. The slide is preserved permanently in this fluid. This is obviously one of the limitations of the method, since the slide has to be examined on each occasion in the fluid medium in a Petrie dish. For storage I use grooved glass staining jars. One could, of course, mount in balsam and so obtain permanent solid mounts, but this would be at the expense of just that optimum of transparency which makes the method so valuable; and after all, since it is a laboratory method and not a class method, the inconvenience, except for storage, is not very great. One can easily mount all the sections of even a 20 mm. pig embryo on one 3 in. by 1 in. slide. It is thus possible readily and rapidly to survey the whole structure of such an embryo in the space of one slide with the advantage of visualising the structure in three dimensions.

I confess that I am not yet satisfied with my staining results. The light haematoxylin stain certainly gives exquisite results, and I have latterly used it exclusively, but it tends to fade in time and some of the series shown are not as good as they were some time ago. Paracarmine is permanent but too uniform in tone and lacking in discrimination.

Professor Hill has suggested alum-cochineal to me but I have not had time to try it. I have little doubt that a suitable permanent stain can be devised.

Although I have chosen, as an example of the employment of the method, the preparation of a series of transverse slices, it is obvious that it is applicable to sections made in any direction and in planes that may be either parallel or non-parallel as desired. Sections of some vertebrate embryos in horizontal planes are most instructive as the sections of larval *Amia* and *Cryptobranchus* exhibited will show.

The preliminary infiltration of celloidin, and the production of a firm celloidin block, are necessary in order to obtain good clean-cut slices. The mounting in gelatin and not in a layer of celloidin is necessary because the clearing fluid softens and gradually dissolves the celloidin whilst the section itself remains fixed in the gelatin layer. The staining of the celloidin slices before mounting on the slide in the gelatin is necessary since the latter would retain the stain or only imperfectly discharge it. I may point out that quite irregular uncut fragments, or blocks sliced in irregular directions, may be stained and mounted in quite similar fashion, often with excellent results. In fact celloidin blocks may be carved in a variety of ways to bring out special structural features with great advantage, so long as they are not so thick as to become too opaque after even light staining. I may add that whole mounts of chick embryos lightly stained and fixed on the slide by gelatin and then passed into Spalteholtz' fluid are immensely superior to the ordinary balsam mounts of such objects, although, of course, they are not suitable for students' class preparations.

It is not suggested that the adoption of this method will in any way replace the customary systematic study of ordinary serial sections. The method permits of the employment of only quite low power magnification and the finest structural detail is therefore inaccessible by its means.

But I do suggest that a complete exploitation of the structural arrangements of any moderately advanced embryo should now, if possible, include the preparation of one or more Spalteholtz series of thick sections in addition to the usual thin series in the three planes, transverse, sagittal and coronal.

For all forms of study by the method described it is evident that the stereobinoocular microscope is practically indispensable. It is desirable to have an intense illumination of the field, and a convenient source of illumination. I have found the ordinary method of illumination by a substage mirror very troublesome in using the binoocular microscope. It is often difficult to get both fields evenly illuminated. The mirrors supplied with the instruments are invariably too small. I have devised a convenient microscope table which permits of constant and adequate direct illumination from below and at the same time enables one to dispense altogether with a special stage; the top of the table forms a stage of far simpler and more effective character.

The table can also be used for work with reflected light by employing any of the excellent electric microscope lamps, for which an alternative switch can be provided.

# THE ORIGIN OF THE HEART AND BLOOD VESSELS IN *FELIS DOMESTICA*

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## GENERAL INTRODUCTION AND METHODS

THE following observations were made on a beautiful series of cat embryos in the collection of Prof. J. P. Hill, and I wish to express gratitude to him not only for permission to work on the material but also for his guidance and criticism, which have served as a stimulus throughout my work. I am indebted to the Scientific and Industrial Research Committee for a grant which has enabled me to devote part of my time to research during Sessions 1919-20, 20-21, and 21-22.

In this paper I shall deal only with very early stages (4-5 somites to 15 somites). The problems considered are therefore those of the actual origin and very early development of the heart and blood vessels. With regard to the heart, I was anxious to find out how far the processes described by Wang<sup>(15)</sup> for the ferret occur in other mammals. In this paper Wang describes a "primary union" of the heart primordia and states "It should be specially noted that the term 'primary' proposed signifies that the right and left parts separate from one another and are again fused by a secondary union" (p. 169). Unfortunately Wang has misunderstood and actually misquoted my paper on the early development of the heart in Marsupials. He gives the impression that I also found the same "primary" union in *Dasyurus viverrinus*, which is contrary to fact. The principal object of the present study is to give an accurate account, based on a closely graded series of stages, of the early development of the heart in a Mammal. The material also affords an opportunity for observing the earliest stages of development of the blood vessels. In recent years the problems of vasculogenesis have received a considerable amount of attention, and, as the result of the work of a number of American anatomists, the theory of the origin *in situ* of the vessels of the embryo has been definitely established. It is unnecessary to give here an account of the recent work on the subject as McClure<sup>(6)</sup> has given an admirable summary so recently as March, 1921. The relative merits of the method of injection and that of study of serial sections have been freely discussed by various authors. Obviously, for the study of the development of the vascular system as a whole, both methods are necessary. For the purpose of discovering the actual origin of the cells which line the blood vessels it is clear that the injection method is inapplicable.

The present paper deals with a series of ten embryos. The sections are all  $10\mu$  thick. I have made one or more graphic reconstructions of each embryo



which is cut transversely, and these are reproduced here as text-figures. The main object is to make clear the relations of the heart, pericardium and gut. I have, however, also graphed the aorta and aortic arch and the umbilical vein from their inception onwards. In so doing I have repeated some of the work published by Schulte in 1914<sup>(12)</sup>, and my results in general simply confirm his. I have not, however, followed his precedent and distinguished "hyperentodermal" mesenchyme cells from vasofactive cells. In the material I have studied, I cannot distinguish these two types of cells. Moreover, Schulte's account of their characteristic features appears to me unconvincing. Referring to the distinction between hypentodermal mesenchyme and vasofactive cells, he says (pp. 42, 43): "These (vasofactive cells) are readily distinguished from the other mesenchyme cells by their transverse position, in addition to their slightly more abundant protoplasm and slightly paler stain....The transverse position of the vasofactive cells requires explanation. They stand out clearly against the other mesenchyme cells which have their long axis in general radial, and are further distinguished by their rather deep position, near or in the almost cell-free interval between the bulk of the mesenchyme and the compact layer of parietal mesoderm." Apparently he means this distinction to apply also to hyperentodermal mesenchyme and vasofactive cells. Unfortunately he does not explain to what plane the vasofactive cells lie "transverse" or the mesenchyme ones "radial" and his figures do not make this distinction clear. In his fig. 24, plates of "mesenchyme cells" (green) form the continuation of "anlages of the dorsal aorta" and in reference to fig. 24 he says (p. 48): "A second endothelial sac in the aortic lines is situated just cephalad of the somites, ending near the first somite in continuity with a flattened plate of mesenchyme cells." It seems evident that such plates of mesenchyme cells must become absorbed in the formation of the aorta and if so they are, *ipso facto*, vasofactive cells. In any case no distinction in position or staining capacity can have greater weight in identifying a cell as vasofactive than the fact that such a cell does contribute to the formation of the wall of a blood vessel. Schulte appears to me to have based his distinction on the grounds of position and staining capacity and to have failed to justify this distinction when tracing the subsequent fate of the cells. Furthermore, in all probability the vasofactive cell is simply a modification of the mesenchyme cell so that the distinction is in any case of minor importance. In making my reconstructions I therefore included as nearly as possible every individual cell which lay between entoderm and mesoderm in every stage. A study of the series of graphs reproduced in this paper shows that these cells disappear gradually and their place is taken by blood vessels; it is therefore natural to conclude that these cells do form the walls of the blood vessels, and if so, they are vasofactive. The majority of the loose "hyperentodermal" cells (adopting Schulte's term for the moment) thus undoubtedly contribute sooner or later to the vascular system and I shall therefore use the term vasofactive for them, though it is obvious that a few cells may be erroneously included in the graphs

and descriptions under this name. This error will, I think, have no bearing on any point under discussion.

The accurate representation of so many individual cells requires the use of a fairly high power and the process is rather laborious even for a small number of embryos. I adopted a simple method of graphing which is perhaps worth a brief note. I selected a lens and eyepiece giving a good magnification (a Zeiss 8 mm. and No. 6 ocular were used throughout) and a convenient ocular micrometer. The value of the unit of this scale with the given lens and eyepiece may be taken as  $x$  mm. (in this particular case  $x = .008$  mm.). If now we treat each unit of the micrometer as a millimetre, it is equivalent to multiplying each measurement by  $1/x$  (in this case = 125). Using millimetre squared paper and taking the median groove on the brain plate as an axis we can plot a cell which is situated at a distance from the middle line of 30 units on the micrometer as 30 mm. from the axis. If we plot each section ( $10\mu$ ) at a distance of 1.25 mm. from the preceding section, we obtain a fairly accurate graphic reconstruction at a magnification of 125, without multiplying each measurement. This is a great saving of time when each graph represents some hundreds of measurements. Obviously its ease depends on the value of the micrometer scale, but by the use of different lenses it is generally possible to get a condition in which the method is practicable. Moreover, a small error, if produced, is generally of no importance as it remains constant throughout a given series of graphs and in a case like the present one, will have no effect on conclusions. In the case of endothelial tubes, blood vessels and vasofactive cells, each section was carefully graphed, but for the outlines of the gut, pericardium and myocardium it was generally possible to get a fairly good outline by graphing every fourth section.

In the graphs each cell is represented by a dot; unless otherwise stated, all the cells lie between the mesoderm and entoderm.

#### DESCRIPTIVE PORTION

*Stage I. Felis domestica* (31.3.09, C.), 4-5 somites.

Fig. 1<sup>1</sup> represents a graphic reconstruction of the pleuro-pericardial mesoderm and the vasofactive cells of the right side of this embryo. The pleuro-pericardial canal does not yet possess a continuous lumen, but its position is marked by a thickening of the mesoderm which shows a tendency to split into dorsal and ventral layers. The outline of this mesoderm is represented by a broken line in the figure (*P.p.m.*), the transverse lines indicate the absence of a lumen, the interruptions in these lines represent the occurrence of a cavity.

<sup>1</sup> N.B. In all the graphs the following conventions have been observed:

Outlines of the pericardium and myocardium are indicated in fine broken lines.

Outlines of the gut are represented in heavy broken lines.

Outlines of the brain and layers of ectoderm are represented by an unbroken line.

Vasofactive cells are shown as dots.

Blood vessels and angiocytes are represented by solid black.

All graphs are reproduced at a magnification of 62.5.

It is thus seen that the pleuro-pericardial mesoderm is recognisable as a continuous horseshoe around the anterior end of the embryo, reaching its maximum development at the level of the first somite. Small, isolated clefts are present in the mesoderm throughout the extent of the horseshoe, and in the region of the greatest extent of the pleuro-pericardial cavity a continuous lumen is present. Behind this region the pleuro-pericardial canal narrows abruptly and becomes unrecognisable at the level of the posterior margin of the third somite.

The vasofactive cells in the head end of the embryo may be seen to be grouped in two main lines, the one nearer the median line representing the future dorsal aorta, the lateral one being the primordium of the endothelial heart tubes and vitelline veins. Only in the anterior end of the aortic line is a definite, hollow vessel present (*A.D.A.*). It is easily seen from the graph that the vasofactive cells of the aorta fall into anterior and posterior positions, separated by a gap of about 100 mm. This interruption in the line of the aorta is recognisable in each of the early embryos figured and is also seen in some of Schulte's (12) figures. The vasofactive cells of the anterior portion of the aorta are not so numerous as those of the posterior, which moreover become denser as we pass backwards. It is a matter of considerable difficulty to determine the exact site of origin of the cells of the aorta line, but the appearances in this embryo and in the

7 somites and 8 somites stages are fairly conclusive in regard to the anterior portion of the aorta. The vasofactive cells in front of the gap in the aorta have every appearance of arising directly from the head mesoderm which is here fairly sparse (fig. 2). In the region of the gap, the mesoderm is distinctly more closely packed and less thick dorsio-ventrally. It is noteworthy that the medullary plate in this region is flat and widely open, whereas both in front and behind the gap in the aortic line, medullary folds rise up to a greater extent. This fact probably accounts for the compactness of the mesoderm and possibly also for the absence of vasofactive cells in the aorta line. Probably the cells in the aorta line behind its interruption and in front of the first somite also arise from the mesoderm

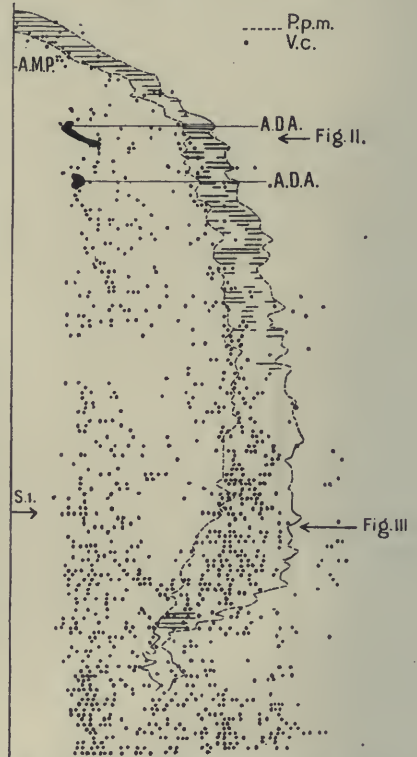


Fig. 1. *Felis domestica*, 4-5 somites (31.3.09). Stage I. Graphic reconstruction of the pleuro-pericardial mesoderm and vasofactive cells of the right side of the embryo. The solid portions of the pleuro-pericardial mesoderm is indicated by lines drawn parallel with the sectional plane. The region where the canal is developed is left unlined. The arrow marks the anterior border of the first somite.



lying immediately dorsal to them. In the region of the somites many of the cells of the aorta lie directly ventral to the somite and, as pointed out by Schulte (12), appearances do not suggest the origin of vasofactive cells from

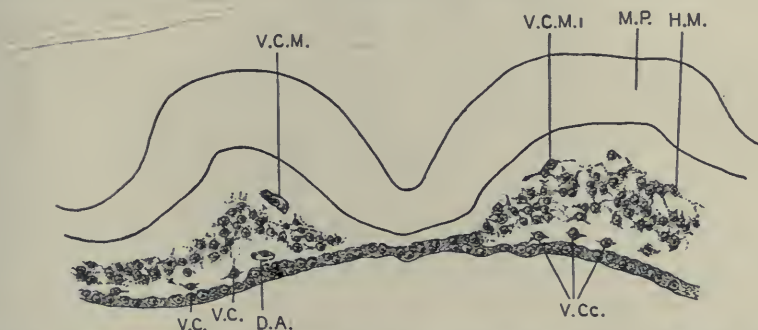


Fig. 2. *Felis domestica*, 4-5 somites (31.3.09). Transverse section. In position indicated in fig. 1.  $\times 130$ .

somites in such a stage as this. On the other hand, in this region both the somitic stalks and the splanchnic mesoderm appear to be active in producing vasofactive cells and it seems possible that the cells of the aorta have arisen laterally and migrated towards the middle line (see fig. 2).

Scattered cells lie between the two main lines of vasofactive cells which at the level of the second somite are connected together by a network of cells. The cells destined to form the endothelial heart tubes are scattered throughout the antero-posterior extent of the pleuro-pericardial mesoderm, reaching actually to the middle line anteriorly. They become most dense in the region of the somites; where they also become continuous with those of the extra-embryonal area and with the aortic line. Behind the portion represented in the graph, the vasofactive cells gradually become less concentrated.

At the anterior end of the head of this embryo there are a few vasofactive cells which are destined to contribute to the formation of the vena capitis

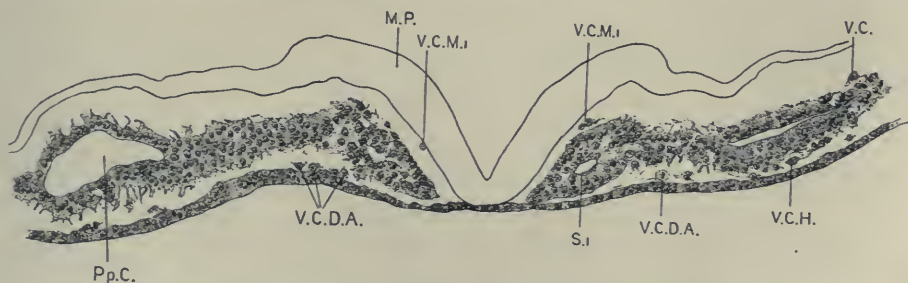


Fig. 3. *Felis domestica*, 4-5 somites (31.3.09, C.). Transverse section in region of first somite (position shown in fig. 1).  $\times 130$ .

medialis. Some of these are shown in fig. 2 (*V.C.M.*), where on one side of the embryo the cells are actually grouped so as to surround a small lumen. These cells occur in the region of maximum development of the dorsal aorta (i.e.

where it actually forms an angiocyst), but are separated from it by a continuous layer of head mesenchyme. Moreover, in some sections the appearances point very definitely to the direct origin of such cells from the dorsal surface of the head mesenchyme. In the following stage, the same appearances will be noted.

This embryo, and, indeed, all this series, show a number of cells between the mesoderm and the ectoderm such as are described by Schulte (12). In the head region these all appear to belong to the vena capitis medialis; in the region of the somites many of them arise from the somatic layer of the mesoderm of the pleuro-pericardial canal, but others are situated close beside the neural tube in the position characteristic of the vena capitis medialis and its posterior continuation (fig. 3).

*Stage II. Felis domestica. 31.3.09. A. and B., both embryos, having 7 somites.*

Fig. 4<sup>1</sup> represents a graphic reconstruction of the pleuro-pericardial canals, aorta, endothelial heart tube and vasofactive cells of the left side of embryo *A*. The outline of the myocardium which is now beginning to develop is also represented. The relations of the parts in median longitudinal section are shown diagrammatically in fig. 4*a*.

The pleuro-pericardial canal is now luminated throughout the greater part of its extent, but a small portion in the middle line is still solid. It resembles that of the preceding stage, but the narrow anterior portion has become longer in antero-posterior extent, and the posterior expansion is wider than that of Stage I. If the anterior border of the first somite be taken as a fixed point, it is obvious that growth in length has occurred in the head region.

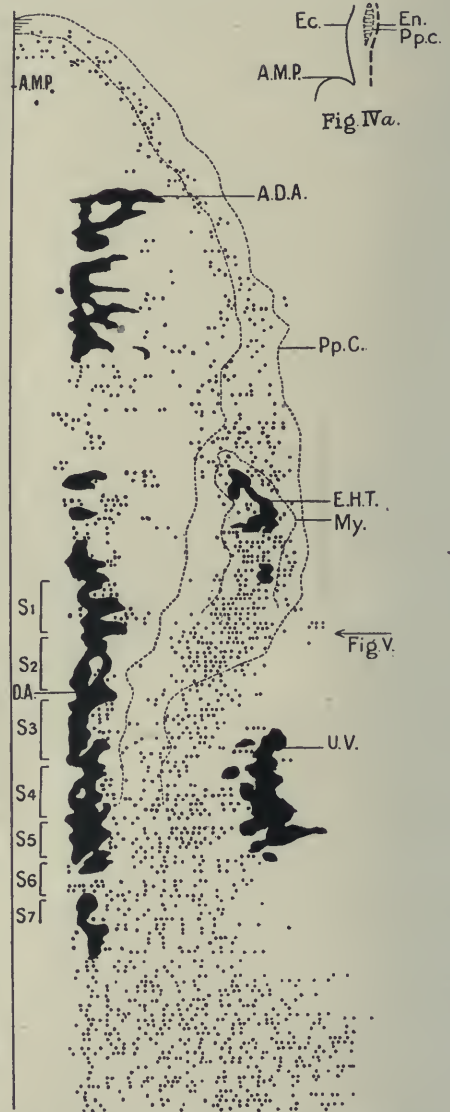


Fig. 4. *Felis domestica*, 7 somites (31.3.09, *A*). Stage II. Graphic reconstruction of the pleuro-pericardial canal, myocardium, vasofactive cells, dorsal aorta and endothelial heart tubes of the left side of the embryo.

Fig. 4*a*. Diagrammatic longitudinal section through the anterior end of the embryo.  $\times 62.5$ .

<sup>1</sup> In figs. 4, 6, 7, 10, 12, 13, for *U.V.* read *V.V.* (vitelline vein).

The dorsal aorta has now become converted into a continuous vessel through a considerable portion of the embryo. In the head region, it is somewhat irregular with lateral offshoots—the descendants of the scattered vasofactive cells between the aorta line and the heart line in the previous stage. These in some cases anastomose with each other. In this embryo we see again a well-marked interruption in the aorta, with only a few vasofactive cells beginning to bridge this gap. The relations of the mesoderm and of the brain plate in this embryo are similar to those in Stage I, i.e. the interruption in the aorta corresponds with a flattened region of the medullary plate and a denser and dorsi-ventrally thinner portion of the mesoderm.

It may be noted here that the dorsal aorta in the region of the somites instead of occupying a mechanically favoured position, as described by

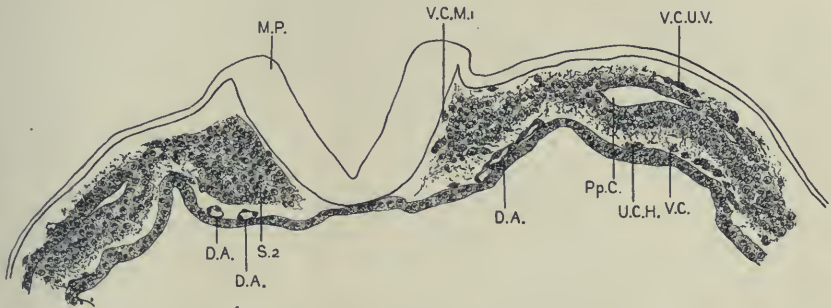


Fig. 5. *Felis domestica*, 7 somites (31.3.09, A.). Transverse section through the first somite on one side and the first intersomitic cleft on the other.  $\times 130$ .

Bremer in the rabbit, lies beneath the somite at its point of maximum depth (see fig. 5).

The vasofactive cells of the heart and vitelline veins are most numerous in the region of the posterior somites, where they extend across a wide zone bounded by the aorta on the median side. At the level of the first and second somites the cells become limited to a strip underlying the pleuro-pericardial canal and penetrate right to the middle line slightly behind the median portion of the canal. Immediately in front of the first somite a portion of endothelial heart tube is definitely established, and this lies in a typical myocardial gutter. The extent of the myocardium is also shown in fig. 4.

Much confusion occurs in the literature of the early development of the heart, owing to the impossibility of drawing a clear line between the portions of the endothelial tube destined to form heart and vitelline vein respectively. Wang (15) uses the term "vitelline vein" for even the anterior portion of the structures commonly called lateral heart tubes (pp. 120, 169, etc.) and also applies the term to structures which I described as lateral heart tubes in *Dasyurus* (pp. 123, 133). Moreover, in fig. 18, he shows a "vitelline vein seen through the pericardium" and obviously situated in a deep myocardial gutter. Observations on slightly later stages of Amniote embryos show that the



ventricular region can be distinguished from the atrial region by the fact that in the former the myocardium is separated from the endothelium by a space which is bridged, as development proceeds, by strands of protoplasm which foreshadow the thick muscular walls of the ventricle (see (7), fig. 14), whilst in the auricular region the myocardium is closely applied to the endothelium (see (7), figs. 17 and 18). In *Perameles* ((7), fig. 9), *Dasyurus* ((7), fig. 24) and *Felis*, as well as in the ferret ((15), fig. 18), this distinctive feature of the ventricle is noticeable even before union of the lateral heart tubes. It therefore appears correct to refer to that region which is situated in a definite myocardial gutter as a lateral heart tube rather than as a vitelline vein. In my previous paper I described the endothelial tubes from the bulbus aortae anteriorly, to the opening of the Cuvierian ducts posteriorly, as lateral heart tubes, and I think that the whole of this portion of the endothelial tube is destined to be converted directly into the median heart.

In the *Felis* embryo now under discussion, the only portion of heart tube present shows the features characteristic of the ventricular region and we may therefore assume that the bulbo-ventricular portion is the first part of the heart to develop in *Felis*.

The myocardial gutter becomes shallow and disappears where the endothelial tube passes over into scattered vasofactive cells. At the level of the third and fourth somites, a portion of the vitelline vein is completely established. It follows the antero-posterior line of the lateral heart tube and so lies lateral to the pleuro-pericardial canal which here curves in towards the middle line.

In both embryos of this stage, portions of the vena capitis medialis are present and in some places a tubular piece of it extends through nine or ten sections.

At the level of the cleft between the first and second somites on the left side of the embryo, there occur a few cells dorsal to the somatic mesoderm of the pleuro-pericardial canal (see fig. 5, *V.C.U.V.*). These represent the first trace of the dense mass of vasofactive cells which develop in this region and give rise to the capillaries from which are developed the Cuvierian duct and the umbilical vein (cf. Schulte (12)). On the left side of the section represented in fig. 5, a single cell between the somite and the neural tube represents the continuation of the vena capitis medialis of this region.

The vasofactive cells continue for some distance behind the region shown in the graph (actually through about .9 mm.), and then disappear. There is no aorta established behind the region depicted in the graph.

*Stage III. Felis domestica* (31.3.09, *D.*), 8 somites.

Fig. 6<sup>1</sup> represents a graphic reconstruction of the pleuro-pericardial canal, endothelial heart tube, aorta and the vasofactive cells of the anterior end of this embryo, which resembles the last stage very closely. The pleuro-pericardial canal is still not luminated in the middle line; it has increased slightly in width throughout the whole extent of its lateral limbs. Two distinct portions of the

<sup>1</sup> See footnote, p. 110.

dorsal aorta are again recognisable and a considerably greater length of the endothelial heart tube is now established. The myocardium has also increased in length and a comparison of figs. 4 and 6 indicates that differentiation of myocardium has taken place both anterior and posterior to the portion existing in Stage II. The endothelial heart tube is continuous posteriorly with a short portion of vitelline vein, but this is not yet connected with the capillaries of the vitelline network. Vasofactive cells lying below the pleuro-pericardial canal continue forwards but do not actually reach the middle line in this embryo.

The relations of the brain plate to the ectoderm and entoderm of the pro-amniotic area and to the pleuro-pericardial canal are somewhat peculiar (see fig. 6 *a*). The brain plate in the middle line is much sunk relatively to the ectoderm lying in front of it; laterally the medullary folds rise up level with the non-neural ectoderm. This elevation of the proamniotic region may be interpreted as a head fold of the amnion; if so, it is precociously developed in this embryo, for it is not present in any other stage described in this paper. It may be noted here that an amniotic tail fold is present in this embryo.

In this stage, as in the embryos having 7 somites, traces of the vena capitis medialis are present, both in the region of the fore brain and in that of the somites, but this vein shows no advance on the preceding stage.

At the level of the first somite, the lateral and ventro-lateral walls of the pleuro-pericardial canal, as well as the dorsal wall are actively producing cells. From their subsequent history it appears that these cells contribute to the formation of the group of capillaries from which the umbilical vein, Cuvierian duct and posterior cardinal vein are all derived. The early development of the umbilical vein has already been described by Schulte (12).

*Stage IV. Felis domestica*, 9 somites (8.2.10, *A.*), *G.L.* 3.6 mm. (neglecting posterior end which was bent under).

The most marked step which has occurred since the preceding stage is the

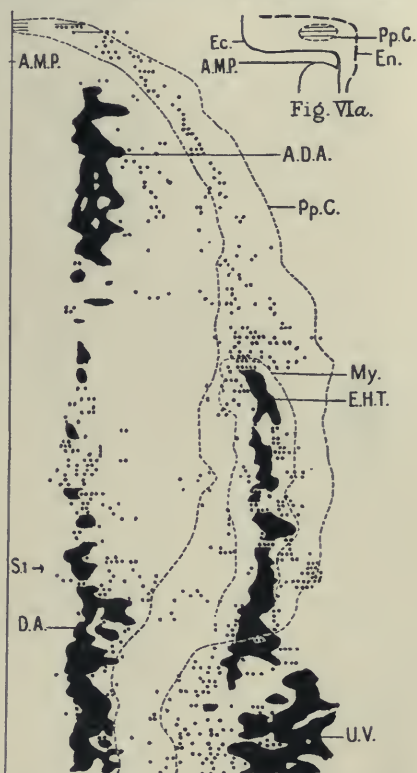


Fig. 6. *Felis domestica*, 8 somites (31.3.09, *D.*). Stage III. Graphic reconstruction of the pleuro-pericardial canal, myocardium, vasofactive cells, dorsal aorta and endothelial heart tube of the left side of the embryo.

Fig. 6 *a*. Diagrammatic median longitudinal section through the anterior end of the embryo.

development of a head fold, resulting in the presence of a small crescentic fore gut. The brain, whose anterior border is indicated in Fig. 7<sup>1</sup> (*A.M.P.*), has grown forward so that its anterior end now lies in front of the anterior wall of the pericardium, instead of behind its posterior border as in the preceding stage. The median portion of the pericardium has increased considerably in antero-posterior extent, and is luminated throughout. Comparison of figs. 6 and 7 shows that the shape of the pleuro-pericardial canal has changed considerably, for whereas in Stage III the widest part of the canal occurs some

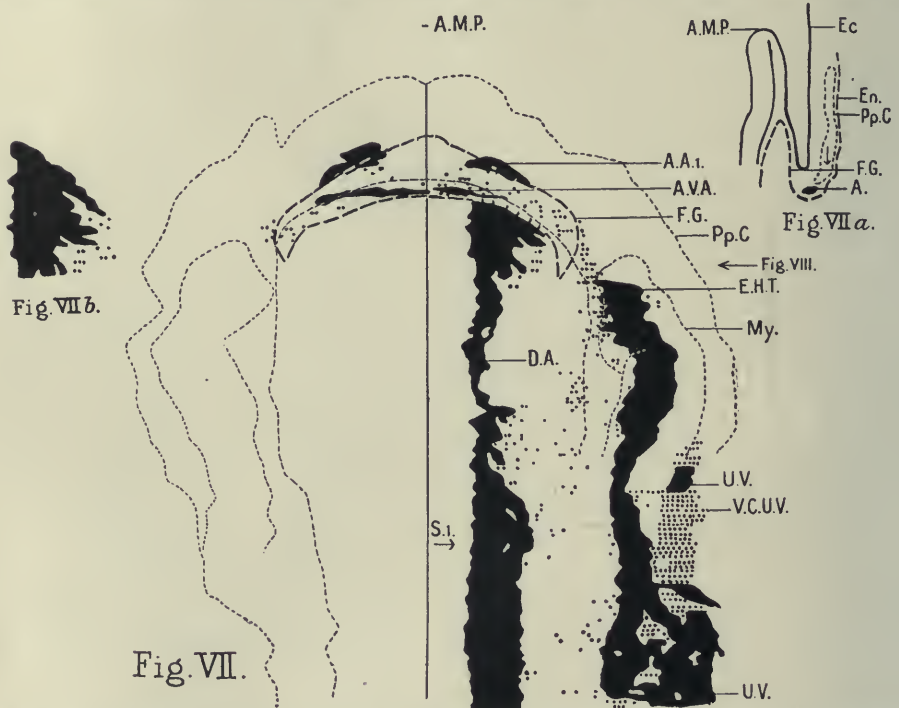


Fig. 7. *Felis domestica*, 9 somites (8.2.10, A.). Stage IV. Graphic reconstruction of the fore gut, pleuro-pericardial canal, myocardium, dorsal aorta, endothelial heart tubes, etc. (left side of embryo on right in figure). Pericardium and myocardium are incomplete on the right side of the figure.

Fig. 7 a. Diagrammatic median longitudinal section through the anterior end of the embryo.

Fig. 7 b. Dorsal view of the anterior end of the dorsal aorta.

distance behind the antero-median limb, in Stage IV, it is situated directly behind this portion. The myocardium has not increased greatly in length; it lies as in Stage III in the region of greatest expansion of the pleuro-pericardial canal and therefore it also is situated much nearer to the antero-median limb than in the preceding stage. It should be noted that in both stages, III and IV, the first somite lies near the posterior end of the differentiated myocardium (cf. figs. 6 and 7).

The endothelial heart tube is now continuous with a wide vitelline vein

<sup>1</sup> See footnote, p. 110.



posteriorly, and runs forward to shortly behind the anterior intestinal portal. It stops short abruptly but anterior to this there are a number of vasofactive cells and on each side of the middle line, immediately in front of the anterior intestinal portal, there is a small angiocyst. These are very thin-walled and slender and lie isolated, posterior to the median limb of the pericardium.

The relations of the pericardium to the gut and fore brain are best understood by reference to the diagrammatic longitudinal section (fig. 7 *a*). From this it will be seen that the fore brain projects freely in front of the gut which is short, whilst the pericardium lies entirely ventral to the ectoderm underlying the head; thus it is situated in front of the ectodermal wall of the head-fold bay, instead of lying between that and the anterior intestinal portal. Moreover, it thus comes to lie between ectoderm and entoderm, instead of lying between two layers of entoderm as it usually does. The small angiocyst is situated entirely posterior to the median pericardium.

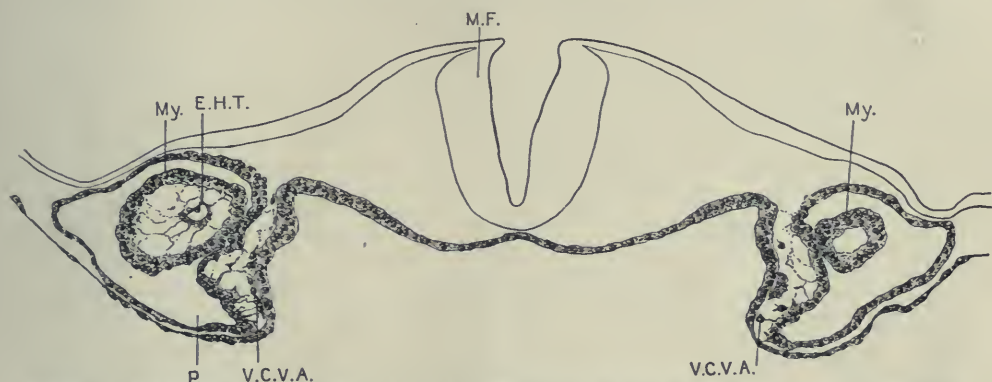


Fig. 8. *Felis domestica*, 9 somites (8.2.10, A.). Transverse section through the anterior extremity of the lateral heart tubes in the position indicated in fig. 7.  $\times 100$ .

The myocardium at its anterior extremity is entirely detached from the pericardium for a few sections and here surrounds the blindly ending endothelial heart tube (see fig. 8). The vasofactive cells lying outside the pericardium in fig. 8 (*V.C.V.A.*) are continuous with the endothelial heart tube and represent the primordium of the ventral aorta in that region.

In the anterior portion of the lateral heart the endothelium and myocardium are widely separated, but the space between them becomes less as we pass backwards.

The dorsal aorta is greatly enlarged at its anterior end and extends to the anterior wall of the fore gut, whilst a slight prolongation of the vessel on to the ventral face of the fore gut is present. This represents the antero-ventral portion of the first aortic arch. The aorta continues back into the region of the somites where it attains a considerable size and lies under the somite itself not under the somitic stalk. The wide anterior and the trunk portions of the aorta are joined by a slender irregular vessel which has now bridged the gap between the two detached parts of the aorta seen in the preceding stage.

A slender vena capitis medialis is present lying alongside the fore brain and opening into the anterior extremity of the dorsal aorta. It is not extensive, but isolated portions of it are recognisable both in the anterior and the somitic regions.

The primordium of the umbilical vein has increased considerably and in a few sections the cells thereof are so arranged as to surround a lumen. A continuous vessel is not, however, established.

This stage then is one in which there are well-developed paired endothelial heart tubes, surrounded by myocardium. Portions of the ventral aorta are present as strings of vasofactive cells and as one isolated angiocyst on each side of the middle line, but these are not continuous either with each other or with the dorsal aorta so that the first aortic arch is incomplete.

A small head fold is developed in consequence of the forward growth of the brain plate, but the pericardium has not yet attained its normal position in the lip of the anterior intestinal portal, but lies entirely outside of the head fold.

The lateral hearts are further forwards relatively both to the brain plate and to the median pericardium than in the preceding stage, but they retain approximately the same relation to the first somite. As the myocardia have not increased much in length it appears that this change in relative position is not merely due to growth of the myocardium.

*Stage IV a. Felis domestica* (8.2.10, B.), 9 somites. Cut longitudinally and *in situ*.

This embryo, although it has the same number of somites as Stage IV, shows a distinct advance in the condition of its gut, pericardium and heart. Unfortunately, the sections are very oblique, so that no one is actually median, but that represented in fig. 9 *a* passes more nearly than any other through the middle line of the heart, whilst figs. 9 *b* and *c* are lateral. The brain is partially closed in this embryo, the gut has increased considerably in length. The pericardium has grown both in antero-posterior extent and in dorso-ventral depth and has altered its position so that in the middle line it now lies wholly posterior to the oral plate, in its normal position in the lip of the anterior intestinal portal. On each side of the middle line, however, there is a diverticulum of the pericardium running forwards and lying between the extra-embryonal ectoderm and entoderm beneath the head fold (fig. 9 *b*).

The right and left myocardial tubes are not fused in the middle line. The endothelial tube shown in fig. 9 *c* can be traced continuously from the auricular region through the ventricular limb which passes into the bulbus aortae. The bulbus aortae is separated from the ventricle by a constriction of the myocardium, the bulbo-ventricular sulcus of Schulte (13), but no definite limit between the ventricle and auricle is present. The endothelium of the bulbus aortae on both sides is continuous with that of the ventral aorta, the right and left ventral aortae being now continuous across the middle line (fig. 9 *a*). From the median ventral aorta thus formed there arises the first aortic arch

which is now complete (fig. 9 c, *A.A.* 1). From the anterior extremity of the first aortic arch arises a relatively large vessel, which runs up alongside the brain and is continued backwards for a short distance as the vena capitis medialis (fig. 9 c, *V.C.M.*).

In the region of the somites the dorsal aorta gives rise to small inter-segmental offshoots, closely resembling those described and figured in *Perameles* (7), but these do not yet appear to be connected by a longitudinal vessel.

The conditions in this embryo appear to resemble closely those described and figured by Schulte (13) in his stage with 11 somites. His figures both of the

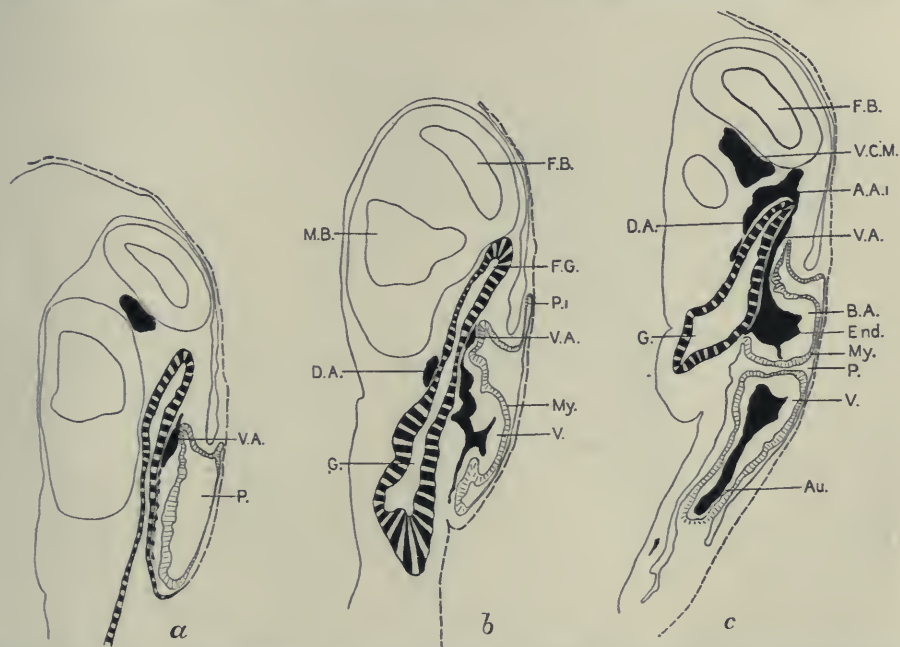


Fig. 9 a, b and c. *Felis domestica*, 9 somites (8.2.10, B.). Stage IV a. Three longitudinal sections through the embryo. Fig. 9 a is nearly median through the heart, fig. 9 b is lateral, fig. 9 c is still more lateral.  $\times 50$ .

endothelial tubes and of the myo-epicardial mantles of an 11 somites cat embryo represent approximately the conditions of the embryo here described.

*Stage V. Felis domestica* (9.5.12, A.), 10 somites, *G.L.* 3.2 mm.

This embryo closely resembles Stage IVa in its general condition. It is unfortunate for purposes of comparison that it is a small embryo, its greatest length being less than that of Stage IV, whilst the distance of the first somite from the anterior end in Stage V is .98 mm. and in Stage IV it is 1.21 mm. The embryo is normal in all other respects, and shows a marked advance on Stage IV though in some respects it is probably earlier than Stage IVa.

In Stage V practically the whole of the pericardium has receded from the



extra-embryonal position which it occupied in Stage IV and only two small solid diverticula of the walls of the pericardium now remain to represent the hollow lateral pockets of the preceding stage.

Fig. 10<sup>1</sup> represents a graphic reconstruction of the endothelial heart tubes, aorta and aortic arch of this embryo, as well as the outlines of the gut, pericardium and myocardium. Fig. 10 *a* represents a very diagrammatic longitudinal section through the embryo.

Comparing this stage with Stage IV, represented in the corresponding figs. 7 and 7 *a*, we see that the fore gut has grown in length considerably, as also has the pericardium. The shape of the pericardium has altered again so that the

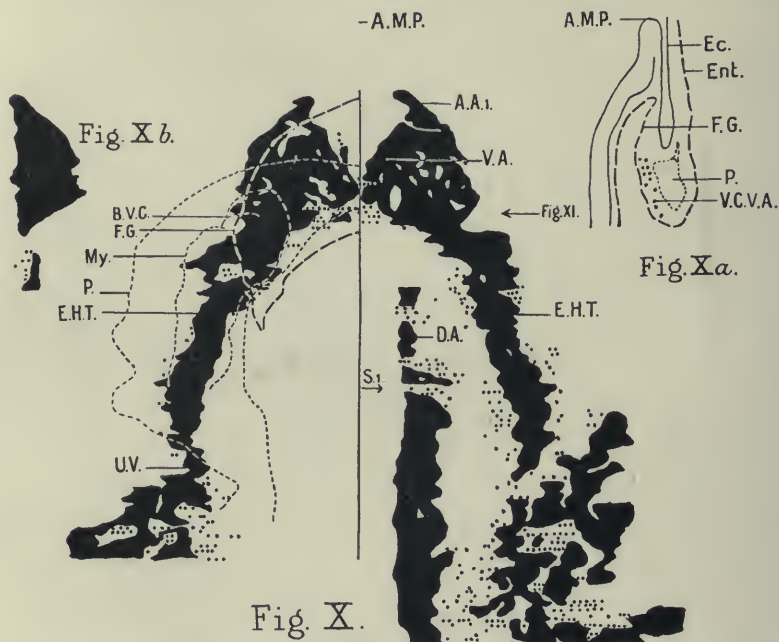


Fig. 10. *Felis domestica*, 10 somites (9.5.12, A.). Stage V. Graphic reconstruction of the endothelial heart tubes, ventral aortae of both sides and the dorsal aorta of the right side and the outlines of the fore gut, pericardium and myocardium of the left side of the embryo.

Fig. 10 *a*. Diagrammatic longitudinal section through the anterior end of the embryo.

Fig. 10 *b*. Dorsal view of the anterior end of the dorsal aorta.

median portion is distinctly shorter and deeper than in Stage IV (cf. figs. 7 *a* and 10 *a*). The lateral limbs of the pleuro-pericardial canals reach their greatest expansion immediately behind the median pericardium. The shape of the anterior intestinal portal has changed from a broad crescent to a reversed U or V. The myocardia are situated relatively further forward than in Stage IV so that their anterior ends now project into the median pericardium and lie ventral to the closed gut (see fig. 11). The well-marked constriction shown in fig. 10 (*B.V.C.*) presumably corresponds with the bulbo-ventricular sulcus of Schulte.

<sup>1</sup> See footnote, p. 110.

The ventral aortae do not communicate across the middle line, but each is a wide vessel, interrupted at intervals by non-vascular loculi and the two aortae approach each other very closely in the middle line. Numerous vaso-factive cells are scattered between the right and left ventral aortae. The first aortic arch is complete and has the form of a very short, wide vessel running along the antero-lateral border of the fore gut to join the dorsal aorta. The anterior portion of the dorsal aorta is a very wide vessel, but it narrows abruptly in the region of the anterior intestinal portal and disappears on both sides of the embryo for a distance of about .04 mm. Behind this gap there is a slender and incompletely established portion of the aorta which, however, becomes larger and perfectly continuous in the region of the somites. Thus in this embryo the original interruption in the line of the aorta which was noticeable in Stages I, II and III has not yet been bridged.

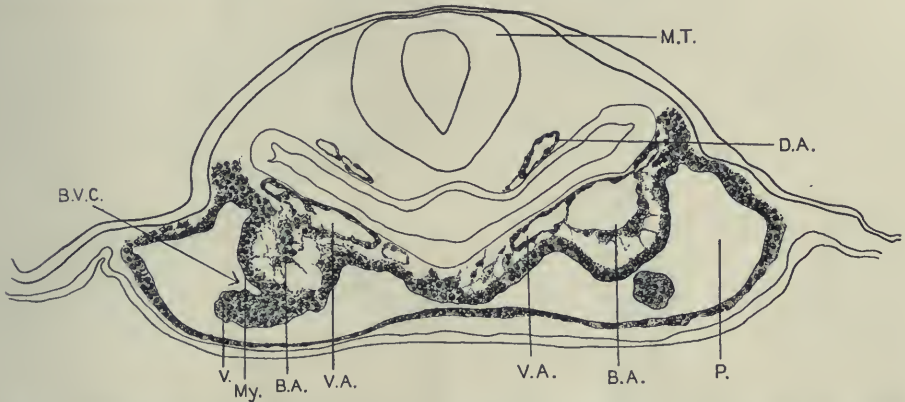


Fig. 11. *Felis domestica*, 10 somites (9.5.12, A.). Stage V. Transverse section through the anterior extremity of the lateral heart tubes, in the position indicated in fig. 10.  $\times 80$ .

A portion of the vena capitis medialis is present, communicating with the dorsal side of the apex of the first aortic arch. Further back in the head there are, as in preceding stages, a few cells close beside the neural tube; these cells are destined to contribute to the vena capitis medialis, but nowhere else is this vessel definitely established. In the region of the somites, there are minute intersegmental offshoots running medianwards and dorsalwards towards the neural tube, but they are not connected by a longitudinal vessel.

The primordium of the umbilical vein now lies entirely dorsal to the pleuro-pericardial canal and more of the cells are now grouped so as to surround a lumen.

*Stage VI. Felis domestica* (B.6.12, D.), 12 somites. Cut longitudinally and *in situ*.

Only a brief reference to this embryo is necessary, as it differs in no important features from Stages IVa and V. The right and left endothelial tubes are fused in the region of the bulbus aortae and appear to communicate with each

other at one or two points in the ventricular region. The myocardia are also fused in the bulbar region but not elsewhere. The ventral aortae are still separate and are smaller more definite channels than in the preceding stage. The first aortic arch is complete and there are traces of the ventral portion of a second. Portions of the vena capitis medialis are present in the fore brain region, but I have failed to trace any connection between this vessel and the dorsal aorta or first aortic arch on either side in this embryo.

This embryo appears to be very similar to that with 12 somites described by Schulte(13).

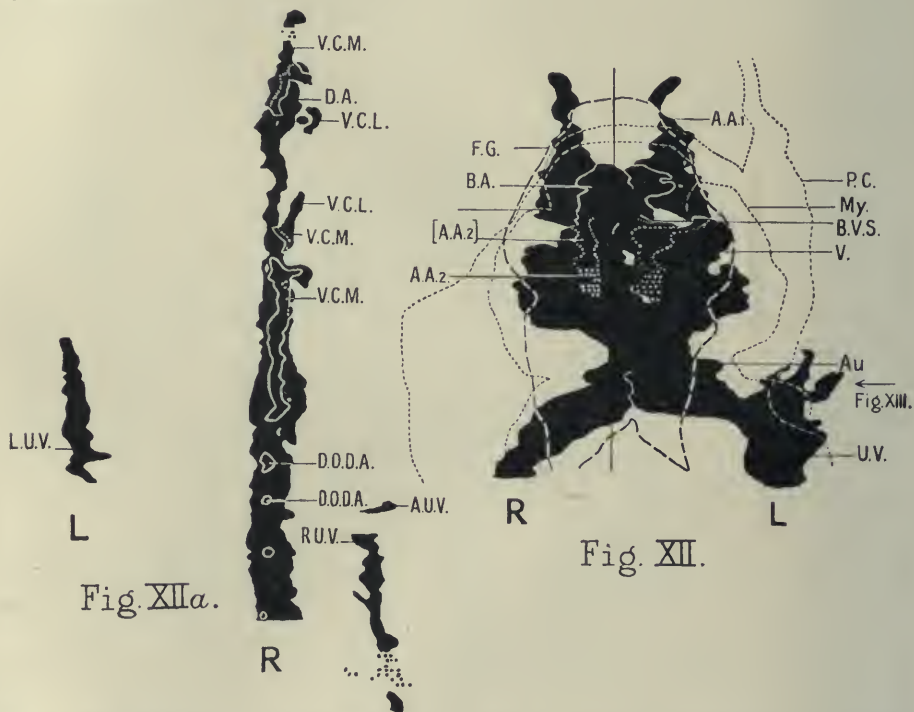


Fig. 12. *Felis domestica*, 15 somites (26.3.09, C.). Stage VII. Graphic reconstruction of the heart, pericardium, fore gut and first aortic arch. The outline of the ventral part of the second aortic arch is indicated represented by a dotted line to indicate that it lies dorsal to the ventricle.

Fig. 12 a. Dorsal view of the dorsal aorta of the right side of the embryo and the umbilical vein of both sides.

Stage VII. *Felis domestica* (26.3.9, C.), 15 somites. *Felis domestica* (11.3.09, E.), 14 somites (cut longitudinally).

Figs. 12 and 12 a<sup>1</sup> represent ventral and dorsal views of a graphic reconstruction of the former of these two embryos, whilst fig. 14 a represents a median and fig. 14 b a lateral section through the second embryo, cut longitudinally.

The condition of the heart, pericardium and blood vessels is simple and stages of this type are so well known that no detailed description need be

<sup>1</sup> See footnote, p. 110.



given. Three main divisions of the heart are easily recognisable, viz. the bulbus aortae, the ventricle and an auricular limb which passes imperceptibly into the vitelline veins. The ventricle is separated from the auricular limb by a well-marked constriction which affects both myocardium and endothelium.

The endothelial tubes are united throughout the bulbus aortae except for a short distance at its anterior end; they are united through most of the ventricular limbs, but separate at two points for a short distance. The myocardia are united also in the bulbus aortae and ventricle, but a groove on the ventral face of the myocardium indicates the line of fusion and in one portion of the ventricle, the two myocardial walls diverge from each other, being here separated by a flat stretch of mesoderm, the middle cardiac plate of Schulte (13) (fig. 4).

The asymmetry described by Schulte in his embryo with 14 somites has made its appearance, but is only slight in this stage; the anterior end of the left side of the ventricle is slightly in advance of that of the right side, whilst in the auricular region the asymmetry is more marked.

The pericardium has the normal form and relations, except for the presence of a peculiar tubular diverticulum on the left side. This runs far forwards, between the extra-embryonal ectoderm and entoderm, lateral to the head of the embryo. It is probably a slight abnormality of no special interest for our present purposes.

The first aortic arch is complete and in both embryos the ventral portion of the second arch is present. From the apex of the first aortic arch a small vessel arises and runs dorsalwards close beside the brain. This vena capitis medialis can be traced forwards dorsal to the anterior end of the head and it also runs backwards for some distance. Just behind the optic vesicle there is present a small portion of the vena capitis lateralis, opening into the vena capitis medialis. Behind this again is a small angiocyst apparently also part of the vena capitis lateralis, but it seems to be completely isolated. Further portions of these veins are present as indicated in fig. 12 *a*. In the region of the somites inter-segmental offshoots are again present, but are not connected by a longitudinal vessel.

The umbilical vein shows a striking asymmetry, lying at the level of the auricular segment on the left side of the embryo, whilst on the right side it is situated in the region of the widely separated vitelline veins (see figs. 12 and 13)<sup>1</sup>.

#### SUMMARY AND CONCLUSIONS

##### 1. Development of the pericardium and heart.

Since the original description by Hensen in 1875 of the bilateral origin of the heart in Mammals, it has been regarded as established that the median heart is derived from lateral heart tubes which, in Mammals, take their origin in the hind brain region by the proliferation of cells from the ventral wall of the pleuro-pericardial canal. These cells become grouped to surround a lumen and the vessel thus formed grows both forwards and backwards and constitutes

<sup>1</sup> See footnote, p. 110.

the endothelial heart tube. At the same time, it causes a bulging of the ventral wall of the pleuro-pericardial canal into its cavity, forming the myocardial gutter or myo-epicardial mantle from which the muscular wall of the heart is developed. It is further recognised that on closure of the gut, the myocardia

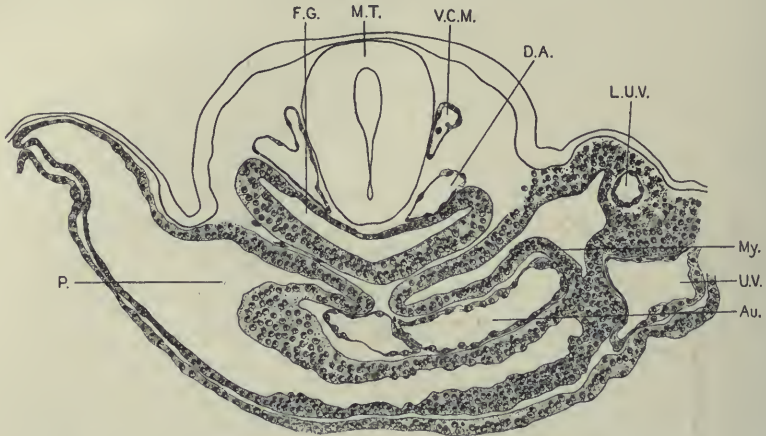


Fig. 13. *Felis domestica*, 15 somites (26.3.09, C.). Transverse section in auricular region of the heart, in the position indicated in fig. 12.  $\times 93$

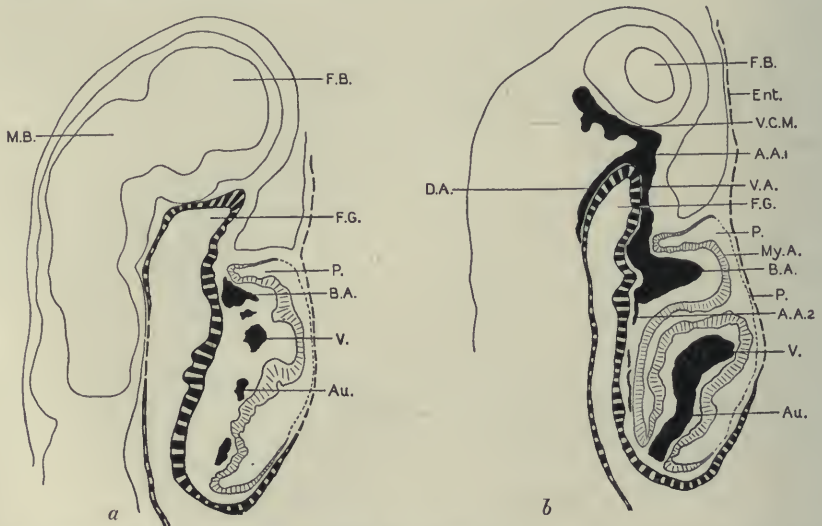


Fig. 14. *Felis domestica*, 14 somites (11.3.09, E.). Stage VII. (a) Longitudinal section, approximately through the middle line of the heart. (b) Longitudinal section through the bulbus aortae, and first aortic arch of the right side of the embryo.  $\times 50$ .

and endothelial tubes are brought into position ventral to the gut, and those of the right and left sides eventually fuse. Various authors (e.g. Rouvière<sup>(9)</sup>, Robinson<sup>(8)</sup>) have discussed the method by which these changes are brought about, but the main outlines of the process have only been questioned by

Wang<sup>(15)</sup> who states (p. 172): "It will be noticed then that there is evidence to show that, at a period before the formation of the fore gut the first rudiment of the heart in the ferret is single and is situated in the median plane of the embryo, caudoventral to the pleuro-pericardial cavity, in the form of a transverse endothelial tube which is destitute of any blood cells. Laterally it is in direct communication with the two vitelline veins one on each side of the embryo." Again (p. 173): "The next phase of development of the heart is represented by the separation of the 'primary' heart rudiment into two distinct endothelial tubes lying closely together one on each side of the embryo, not far from the median plane."

Attention has been drawn above to the confusion caused by the loose application of the term vitelline vein. Wang has applied it in his Stage III to a well-defined endothelial tube, surrounded by a myocardial wall<sup>(15)</sup> (fig. 18), which corresponds exactly with the structure usually described as a lateral heart tube. In his Stage II the pleuro-pericardial canal appears to be incompletely differentiated, whilst the endothelial tube is relatively advanced. There is, however, no evidence in his paper that his "median heart" actually developed earlier than the so-called "vitelline vein." Both the "vitelline vein" and the "median heart" are absent in Wang's Stage I, and are completely established in Stage II so that no direct information is available as to the order and mode of development of these two structures in the ferret. It may be noted that in Wang's fig. 6a (Stage II) the "vitelline vein" is much larger than the "median heart," a fact which suggests that the "vitelline vein" appeared first. Moreover, Wang's median heart rudiment lies caudo-ventral to the pericardium<sup>(15)</sup> (pp. 170, etc.), and appears to correspond exactly with the two angiocysts seen in my Stage 4 (fig. 7) and these lie outside the limits of the heart proper, and form the ventral aorta. Unfortunately, in his fig. 18, Wang does not give the complete outline of the myocardium, but in his figs. 19, *a*, *b*, *c* and *d*, he shows the "median heart rudiment" entirely without a myocardial wall, whereas in fig. 18 he shows a distinct myocardial gutter around the "vitelline vein." The correct interpretation of Wang's material therefore appears to me to be that his "median heart" represents a ventral aorta which has developed and fused in the middle line earlier than it does in most Mammals, whilst the heart proper has arisen in the typical way from lateral endothelial tubes (Wang's "vitelline vein" which makes its appearance between his Stages I and II) and is surrounded by a myocardium of the ordinary type. Moreover, the fact that in Wang's Stage IV the right and left endothelial tubes are separate does not prove conclusively that the heart is first median and later separates into two tubes, for reconstructions of a number of embryonic hearts show that even within a species, there is a great variation in the relative development of different parts of the heart and in the mode of union of the right and left endothelial tubes. The ventral wall of the pleuro-pericardial canal appears to be capable of producing vasofactive cells throughout its entire length and it is evident that if such cells be produced at an early stage right



across the middle line (as is the case in my Stages I and II) a median angiocyst is likely to be produced before the lateral heart tubes reach a position in which fusion is possible. On the other hand, if few endothelial cells arise near the middle line (as is the case in my Stage III) no median angiocyst will be formed prior to the fusion of the lateral heart tubes. The work of Schulte<sup>(13)</sup> and the graphs in the present paper taken together show that in the cat, fusion takes place piecemeal, rather than at one step or even in steady progress cranio-caudally. It is therefore quite possible that in the particular embryo described by Wang as Stage IV, the early development has differed slightly from that occurring in the embryos described as Stages II and III. To this point I will return after discussing the corresponding processes in the cat.

Several other points raised by Wang<sup>(15)</sup> in his paper on the development of the heart in the ferret may be mentioned here. He refers repeatedly to my description of a *Dasyurus* embryo (*Dasyurus viverrinus*, Stage II, 8.5 mm, *A.* in my paper of 1915<sup>(7)</sup>), and on p. 133 he states: "In the *Dasyurus* the endothelial tubes have come actually in contact with each other at their extreme cranial ends and presumably have united across the median plane of the embryo. It should be noted that the significance of this connection between the two vitelline veins across the median plane was not dwelt upon, and was considered only as being remarkable by Miss Parker, who states also 'that lateral and caudal to the median union, each endothelial tube gives rise to the first aortic arch, which follows the antero-lateral margin of the gut almost to the median plane, and there becomes continuous with the corresponding dorsal aorta, the two aortae being well developed at this stage'." The quotation from my paper though in inverted commas is inaccurate, my actual words being "Some distance behind its cephalic extremity, the lateral heart tube gives rise to the first aortic arch, which follows the antero-lateral margin of the gut almost to the middle line and there becomes continuous with the corresponding dorsal aorta, the two aortae being completely established in this stage."

I have re-investigated this question of union of the heart tubes in this *Dasyurus* embryo and find that the right and left tubes are not fused. Professor J. P. Hill, F.R.S., to whom this specimen belongs, has also examined its heart and agrees with this statement. Even if fusion does occur at about this stage in *Dasyurus* (i.e. about Stage II of my paper<sup>(7)</sup>), the fact would not support Wang's view that the first rudiment of the heart is a median structure, for typical lateral endothelial tubes, surrounded by a myocardium are present in an earlier stage as described in my paper (*Dasyurus viverrinus*, Stage I, 7.5 mm.<sup>(7)</sup>).

I greatly regret that in Plate I, fig. 4<sup>(7)</sup>, a line which should have divided the right and left endothelial tubes throughout the greater part of their length, was lost in reproduction. This brought about the inconsistency between the text and that figure to which Wang<sup>(15)</sup> refers on p. 175 (see fig. 15).

With reference to Wang's further criticism (p. 175) that I omitted to state

the magnification of my figures of Stages IV and V and the lengths of these embryos, it may be remarked that I refrained from comparison of lengths between Stages IV and V for several reasons. In the first place the embryos are of different species and are therefore even more liable to variations in size than two embryos of the same species; in the second place, Stage IV is markedly in advance of Stage V in almost every respect except the development of the heart. Stage V is, in fact, very similar to Stage III as regards the development of its brain. For these reasons I did not attempt to make comparable figures of Stages IV and V. I regret very much that I did not make these points clear.

The series of cat embryos described above enables us to get a clear idea of the development of the heart and pericardium from the stage of the appearance of the pleuro-pericardial canals and the origin of the endothelial cells of the heart and aorta up to the complete establishment of a median heart with a recognisable bulbus aortae, ventricle and auricle. The details of the process of fusion of the lateral heart tubes in the cat have been given clearly by Schulte (13), and will not be repeated here.

The first stage in the development of the heart is one in which the pleuro-pericardial mesoderm is recognisable and forms a horseshoe around the anterior end of the embryo, with its median portion shortly in front of the anterior margin of the medullary plate. The median limb of the horseshoe is narrow and the lateral limbs become narrower as we pass backwards, and in the widest part of the pleuro-pericardial mesoderm a cavity is already present.

Vasofactive cells are numerous and occur in greatest numbers in the posterior part of the pleuro-pericardial canal and caudal to this region. Two or three angiocyts in the anterior part of the aorta are the only ones present; the vasofactive cells ventral to the pleuro-pericardial mesoderm extend right to the middle line in front of the anterior margin of the medullary plate.

Development proceeds by the spreading of the cleft constituting the pleuro-pericardial cavity, by the increase in the number of vasofactive cells, and their re-arrangement to form angiocyts, which coalesce to form vessels. These develop along two almost parallel lines one representing the dorsal aorta, the other the heart and vitelline vein. The development of the blood vessels will be dealt with in another section. The endothelial heart tube appears first (Stage II, fig. 4) just in front of the level of the first somite, and there it causes a slight bulging of the ventral wall of the pleuro-pericardial canal, the myo-

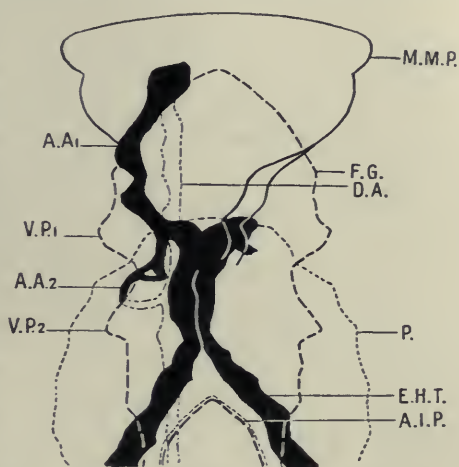


Fig. 15. *Perameles nasuta* (2PA). Outline reproduction of fig. 5, Pl. I, from the "Early development of the heart, etc., in Marsupials" (7).

cardial gutter. In this first developed portion of the lateral heart tube, the endothelium and myocardium are widely separated and it seems probable that this region represents the bulbo-ventricular limb.

The pleuro-pericardial canal expands both in lateral and dorsi-ventral extent and the endothelial heart tubes and myocardia continue to grow both forwards and backwards. If we compare Stages II and III (figs. 4 and 6) we see that the main change that has taken place consists in the conversion of vasofactive cells into endothelial tubes. The curious position of the median limb of the pleuro-pericardial canal in Stage III may be regarded as of no significance in the present connection.

After this stage there follows one of very rapid development. The most important factor in the change of relations occurring between Stages III and IV is undoubtedly the forward growth of the brain. If we take, as a starting-point, Stage II (which is not complicated by a precocious head fold of the amnion), and imagine that the brain plate grows so rapidly that it pushes its anterior border forwards and at the same time the pleuro-pericardial canal increases in the antero-posterior direction, the condition seen in Stage IV is brought about, i.e. a small fore gut is developed, the median limb of the pleuro-pericardial canal is left lying between extra-embryonal ectoderm and entoderm. The vasofactive cells lying caudo-ventral to the median limb of the pleuro-pericardial canal in Stage II are, in Stage IV, converted into two angiocyts which still lie caudal to the posterior wall of the pleuro-pericardial canal, showing that no reversal of the pericardium has taken place up to this stage. At the same time the pleuro-pericardial canal has undergone a considerable change in shape and relations. Its median limb has increased in antero-posterior extent and its lateral limbs attain their greatest width very shortly behind the median limb. Moreover, the myocardia, which have not grown much in length (see figs. 6 and 7), now lie further forwards so that their anterior extremities reach almost to the median pericardial limb of the horseshoe. Whilst part of this change in relative position of the myocardium and pericardium is due to forward growth of the myocardium, it is evident that other factors have been at work. If we note the relations of the myocardium and pericardium to the somites we see that the first somite in both stages lies level with the posterior part of the myocardium, whilst the distance between the first somite and both the anterior and posterior walls of the median pericardium is considerably less in Stage IV than in Stage II.

The explanation of these facts seems to be that the anterior (median) limb of the pericardium is increasing in size at the expense of the lateral limbs and that as it enlarges it also moves backwards. In Stage IV no other changes in the pericardium have taken place, i.e. it has not undergone reversal as described by Robinson (8) nor have its lateral limbs begun to close inwards as described in *Perameles* and *Dasyurus* (7), for the anterior intestinal portal still has a wide crescentic shape, and the vasofactive cells and angiocyts lie posterior to the median pericardium.



Throughout this period, vasofactive cells, wherever they may be, continue to be converted into angiocyts and blood vessels. The presence in Stage IV of two angiocyts near the middle line indicates the manner in which the "median heart" of Wang (15) might be produced, but it may be noted here that in the embryo described as Stage III vasofactive cells do not extend across the middle line in relation to the pericardium. It seems probable that in such an embryo, the development of Wang's "median heart" would be omitted and the completed endothelial tubes might be found separated at a relatively late stage as described by Wang (15) in his Stage IV.

Following on Stage IV in *Felis domestica* there occurs a rapid expansion of the median limb of the pericardium and a change in its position, for in Stage IVa the pericardium lies almost entirely behind the ectodermal limit of the head fold, between that and the entoderm of the anterior intestinal portal. The two angiocyts seen in Stage IV have in Stage IVa united across the middle line and form a ventral aorta which is now continuous with the heart on the one hand and with the first aortic arch on the other. It must be noted that this median vessel has no myocardial gutter surrounding it. It lies at the anterior end of the median pericardium, i.e. in the reverse of its position in the preceding stage. On each side of the middle line a portion of the pericardium has retained its former position between the extra-embryonal ectoderm and entoderm and traces of these lateral diverticula are present in the next stage. This fact sheds light on the process by which the pericardium shifts from its position in Stage IV to that which it occupies in Stages V and VI, for it must take place by the backward growth of the postero-ventral wall of the median pericardium in Stage IV, in the manner indicated by an arrow in fig. 8a coupled with the backward movement of the median pericardium as a whole. This must be imagined as taking place in such a way as to bring about the reversal in position of the ventral aorta between Stages IV and IVa whilst permitting of the "lagging behind" of the lateral diverticula of the pericardium in the extra-embryonal region.

The anterior ends of the myocardial tubes surrounding the endothelial tubes in Stages IVa and V have reached a position in the median pericardium and lie in Stage V (fig. 11) ventral to the closed gut but still separated from each other. From this point the heart tubes in Stage V follow a spirally curved course round the anterior intestinal portal so that their posterior ends lie in the ventral wall of the lateral pleuro-pericardial canal. At the same time, between Stages IV and V the lateral limbs of the pleuro-pericardial canals have converged towards the middle line, so that in Stage V the anterior intestinal portal has the shape of a narrow U instead of the wide crescent of Stage IV.

The process by which the head fold is formed and the lateral heart tubes are brought into position ventral to the newly established fore gut thus consists in the enlargement and backward growth of the pericardium, accompanied by a twisting of the pericardium. This twisting must be due to

differential growth which brings about a complete reversal in the middle line first and thus causes the heart tubes at one period (e.g. in Stage V) to take a spiral course between their anterior ends which lie dorsal to the median pericardium and their posterior ends which lie ventral to the lateral limbs of the pleuro-pericardial canal.

It may be noted that actually in the middle line in Stage V the pericardium is smaller in the antero-posterior direction than in Stage IV. It is, however, deeper in the dorsi-ventral direction (N.B. the embryo described as Stage V is smaller than that described as Stage IV) and a shortening and deepening of the pericardium in the middle line seems to me a natural phase in such a process of back-growth and twisting as I have described.

By a continuation of the process of extension of the median pericardium, accompanied by its rotation, the lateral heart tubes are gradually shifted from the ventral to the dorsal side of the pericardium.

This account of the formation of the head fold merely amplifies that given by Rouvière (9). Robinson (8), on the other hand, attributes a large share in the process of gut closure to the forward growth of the brain. I have previously brought forward evidence against this view (7). The reversal which I have described above I regard as being due not to the forward growth of the head, but to active differential growth of the pericardium.

In the guinea-pig, according to Strahl and Carius (14) (figs. 21, 22, and 22 *a*) and Yoshinaga (16), the processes of gut closure and heart development do not appear to follow exactly the course described here in the cat. The fundamental point of difference between the two forms appears to be that the formation of the head fold takes place at an earlier stage relatively to the development of the heart and pericardium in the guinea-pig than in the cat, i.e. in the guinea-pig the brain plate grows forwards and produces the type of head fold seen in Stage IV of the cat series at a stage when the pleuro-pericardial canal is still very small.

In Stage V (fig. 10) the vasofactive cells ventral to the median pericardium have become converted into a maze of capillaries constituting the ventral aorta and the ventral portion of the first aortic arch which is here complete. These capillaries are very thin-walled and therefore difficult to trace, but they appear not to anastomose in the middle line. As already indicated, however, this appears to be a point of minor importance, as fusion would probably occur if the vasofactive cells develop early in the middle line and might fail to occur if circumstances were unfavourable.

The developmental processes following on Stage V are those concerned firstly with fusion of the right and left heart tubes and secondly with their curvature and both these phases have been adequately described in the cat by Schulte (13). As already remarked, considerable variation seems to occur in details of fusion. Schulte's stages as designated by somites do not agree with mine, but wherever possible I have pointed out a correspondence between his stages and mine. In his 12-somite stage, which shows a stage of heart



development very little earlier than my 15-somite stage, there are points of fusion in the bulbus aortae, whilst in his 14-somite stage there is fusion both in the bulb, the ventricle, and at the cardio-venous angle. In my 12-somite stage there is fusion in the bulb, the ventricular limb and the auricular limb whilst in my 15-somite stage conditions as regards fusion are almost identical with those of Schulte's 14-somite stage, but the heart in my embryo is uncurved, whilst in Schulte's embryo it is markedly curved. The general conclusion is that different embryos vary considerably in the details of the rate of growth of various organs and that fusion occurs differently according to the relative advancement or retardation of the development of the pericardium and heart tubes.

In my previous paper I referred to a suggestion made originally by Prof. J. P. Hill that fusion of the right and left heart tubes is rendered possible by growth in antero-posterior length of the pericardium exceeding its growth in width (7) (p. 492). This explanation was criticised by Wang (15) (p. 174), who slightly misunderstood my point. The process of growth in length of the median pericardium I regard as occurring between the stages of widely separated heart tubes and that of approximated (and possibly curved) tubes, i.e. between Wang's Stages III and IV, between Stages III and IV in my *Perameles* series and between Stages V and VII in the *Felis* embryos described above. Moreover, I expressly stated that "approximation" (not fusion) of the heart tubes results from such a process of longitudinal stretching. The loops into which the heart tubes are thrown are doubtless due to a phase following on this period of growth in length (i.e. a phase following on Stage IV in my *Perameles* series and Stage VII in *Felis*) in which the rate of growth of the heart tubes exceeds that of the pericardium and the former are accordingly forced to curve. Both these stages have occurred between Wang's Stages III and IV with the result, as I believe, that the heart tubes have become first approximated and then curved.

It has been pointed out by Yoshinaga (16) (pp. 302, 303) that in the guinea-pig the phase in which curvature of the heart tubes occurs is preceded by one in which "the myocardial tube grows excessively in the cranio-caudal direction and decreases in lateral width." He further states that the endothelial tubes are brought together in the median plane, where they come to fusion by the extreme longitudinal stretching of that part of the myocardial tube in which the endothelial tubes are enclosed." In my view, growth in length of the pericardium itself is the main factor but as Yoshinaga's figures show clearly that a stretching of the myocardium in the antero-posterior direction also occurs.

## 2. Development of the blood vessels.

The most important recent work on the development of the blood vessels is that of the American anatomists to whom reference was made in the introduction. This work has led to the general acceptance of the theory that the blood vessels of the embryo develop *in situ*, in contrast to the angioblast doctrine of His.



The observations on cat embryos described above in general confirm those of Schulte(12). As his figures and mine show, the earliest stage of vasculogenesis is one in which vasofactive cells occur scattered in the embryo and not connected into an angioblast network as described by Bremer(1) for the rabbit. Moreover, the vasofactive cells in the embryo from a very early stage are grouped in two main lines, an aortic line and a cardiac line. At first there are many cells scattered between these two lines, but as development proceeds, and the aorta and heart tube become definitely established, the cells lying between them disappear. These cells are doubtless used to build up the walls of the vessels and in order to do so some of them must migrate from their place of origin. In the case of the endothelium of the heart, the cells arise apparently directly from the splanchnic mesoderm. They become grouped into clumps and arranged to surround a lumen, retaining approximately their original relation to their place of origin. The aorta in the cat arises as two distinct parts, separated by a gap which is not bridged until a stage having 9 or 10 somites. In the anterior part of the head, in stages with 4 to 7 somites, the medullary plate has risen up slightly into folds, the mesoderm is loosely packed and the cells of the aorta appear to arise directly from the ventral side of this head mesenchyme. Behind this is a region in which the medullary plate in a 4-5 somite stage is perfectly flat, the underlying mesoderm is dense and there appear to be no vasofactive cells in the aortic line. Posterior to this the medullary plate again rises up somewhat. In the embryos with 7 and 8 somites also, there is a widening of the medullary groove and the aorta is interrupted in this region. It therefore appears that the fact that the aorta arises in two portions is simply due to the presence of a region in which the shape of the brain plate causes a certain compression of the mesoderm, and this in its turn inhibits the formation of vasofactive cells.

In the embryo with 9 somites, the medullary folds have risen up more completely and the mesoderm has become less dense. The aorta is here complete, but the site of its former interruption is marked by a reduction in its size.

The vasofactive cells of the aorta as far back as the first somite, appear to arise directly from the overlying mesenchyme. In the region of the somites, however, as remarked by Schulte, it is difficult to determine the exact origin of the vasofactive cells. The somites themselves do not appear to be actively producing them at any stage. On the other hand, it may be noted that in Stage I (fig. 1) there are vasofactive cells in considerable numbers lateral to the somites, whereas in Stage III (fig. 6) there are few of these cells in a similar position. This suggests that a number of vasofactive cells arise lateral to the aortic line and migrate towards that line. The sectional appearances also confirm this view, for in Stages I and II in the somitic region there are numerous vasofactive cells arising from the splanchnic mesoderm, as well as from the somitic stalks (fig. 3). At the same time it is quite possible that, even in these early stages, the somites produce some vasofactive cells in addition to those described by Schulte(12) as being contributed later by the sclerotome. In

many sections, including that represented in fig. 5, the outline of the somites in Stages I and II is not very regular. On one side, in fig. 5, the section passes almost through an intersomitic cleft and here as in other similar sections a cell is seen detached from the paraxial mesoderm and projecting towards the aorta. This suggests that vasofactive cells may arise from the segmented mesoderm. Schulte(12) has suggested that some of the cells of the aorta arise from the paraxial mesoderm before the formation of the somites, but I have found no evidence of this. In Stages I and II in the region posterior to the somites, there is abundant evidence of the origin of vasofactive cells from the lateral mesoderm, cells in all stages of separation being numerous, but the cells lying ventral to the paraxial mesoderm are completely detached and give no clue as to their place of origin.

It seems probable then that the cells which form the walls of the aorta are derived partly from the splanchnic mesoderm, lateral to the final position of the aorta, and partly from the somites (see also Schulte(12)) and somitic stalks.

In the earliest stages described above, the formation of the main vein of the head, the vena capitis medialis, from the mesenchyme lying alongside the brain, can be observed clearly. The vasofactive cells simply become detached from the mesenchyme and a lumen is produced partly by a process of vacuolation of the cells and partly by re-arrangement of the cells to surround a cavity.

Vasofactive cells which are destined to contribute to the posterior continuation of this vessel are seen lying close alongside the spinal cord in the region of the somites. As in the case of the cells of the aorta it is difficult to locate their origin precisely but they probably arise from the somitic mesoderm. Until Stage IV these cells remain isolated, but in Stages IVa and VII a series of intersegmental offshoots from the dorsal aorta can be seen and these run medianwards and dorsalwards towards the spinal cord. Probably both the vasofactive cells lying alongside the nerve cord and the intersegmental offshoots from the dorsal aorta contribute to the formation of a longitudinal vessel lying close alongside the neural tube. This vein in the cat, as in other vertebrates (Salzer(11), Grosser(3), Sabin(10), Parker(7), etc.), contributes to the formation of both the anterior and posterior cardinal veins. In the cat its anterior portion is undoubtedly developed *in situ* and not derived as described by Sabin(10) for the chick from the first aortic arch. In the embryos of *Perameles* and *Macropus* described in an earlier paper(7) it was noted that the vena capitis medialis is present in the head before it becomes connected with the dorsal aorta. It is therefore probable that in these species also the anterior portion of this vein arises *in situ*.

The origin of the umbilical vein *in situ* from the somatic mesoderm has already been described by Schulte(12). From my observations it appears that some of the cells that are destined to contribute to the umbilical vein-Cuvierian duct complex arise from the splanchnic mesoderm and migrate laterally round the pleuro-pericardial coelom to reach their normal position in the splanchnopleure.

## FINAL SUMMARY

1. The heart arises as two lateral endothelial tubes, surrounded by a myocardium and the first portion of the heart to appear is the bulbo-ventricular limb.

2. The mode of union of the lateral heart tubes and their forward continuations varies in different species and in different individuals of the same species. In some cases the right and left ventral aortae are continuous in the middle line before the fusion of the heart tubes takes place (Wang<sup>(15)</sup>, ferret). In other cases the bulbar region of the heart tubes is the first part to fuse. These differences depend mainly on variations in the rate of production of vasofactive cells and the rate of growth of the pleuro-pericardial canal.

3. The formation of the head is initiated by the forward growth of the brain plate, but this by itself produces no reversal of the pericardium, which attains its normal position immediately ventral to the gut by a process of backward movement and enlargement of the pericardium as a whole. The median pericardium increases in antero-posterior and dorso-ventral dimensions partly at the expense of the lateral limbs of the pleuro-pericardial canals and in this way the heart tubes which are at first lateral, come to be surrounded by the median pericardium. At the same time the pericardium undergoes a rotation in such a way that a complete reversal is accomplished first in the middle line and the lateral heart tubes for some time necessarily follow a spiral course between their anterior ends which lie dorsal to the median pericardium and their posterior ends which lie ventral to the lateral limbs of the pleuro-pericardial canal.

4. The lengthening of the fore gut is brought about by growth in antero-posterior extent of the pericardium, accompanied by a backward movement of the anterior intestinal portal.

5. The approximation of the lateral heart tubes is due to the fact that for a time the growth in length of the pericardium exceeds its growth in width to such an extent that there is an actual decrease in the width of the pericardium, so that the lateral heart tubes are brought closer together.

6. After the heart tubes have reached their position in contact with each other, ventral to the gut, they grow rapidly in length and become curved. Fusion of the right and left endothelial tubes takes place at this period, beginning in the bulbar region. It does not take place regularly in an antero-posterior direction, but portions of the bulbus aortae and ventricle remain unfused for some time.

7. Blood vessels arise *in situ*, the cells which constitute their walls being derived from the mesoderm in the region of the vessel. The exact place of origin of the cells of the aorta is not clear in this material, but they appear to arise chiefly from the lateral (splanchnic) mesoderm and migrate from their place of origin to the aortic line.



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ABBREVIATIONS

A. angiocyst; A.A. 1, 2, etc., first, second, etc., aortic arch; A.D.A. angiocyst of dorsal aorta; A.I.P. anterior intestinal portal; A.M.P. anterior margin of medullary plate; A.U.V. angiocyst of umbilical vein; A.V.A. angiocyst of ventral aorta; Au. auricle; B.A. bulbus aortae; B.V.C. bulbo ventricular constriction; B.V.S. bulbo-ventricular sulcus; D.A. dorsal aorta; D.O.D.A. dorsal offshoot of dorsal aorta; E.H.T. endothelial heart tube; Ec. ectoderm; En. entoderm; End. endocardium; F.B. fore brain; F.G. fore gut; G. gut; H.M. head mesoderm; L.U.V. left umbilical vein; M.B. mid brain; M.F. medullary fold; M.P. medullary plate; M.T. medullary tube; My. myocardium; P. pericardium; P. 1 lateral diverticulum of pericardium; P.p.c. pleuro-pericardial canal; P.p.m. pleuro-pericardial mesoderm; R.U.V. right umbilical vein; S. 1, S. 2, etc., somites 1, 2, etc.; U.V. umbilical vein; V. ventricle; V.A. ventral aorta; V.C. vasofactive cell; V.C.D.A. vasofactive cell of dorsal aorta; V.C.H. vasofactive cell of heart tube; V.C.L. vena capitis lateralis; V.C.M. vena capitis medialis; V.C.M. 1 vasofactive cells of vena capitis medialis; V.C.U.V. vasofactive cells of umbilical vein; V.C.V.A. vasofactive cells of ventral aorta; V.V. vitelline vein.

# ON THE MASTICATORY, INTERMANDIBULAR, AND HYOID MUSCLES OF ORYCTEROPUS CAPENSIS

BY F. H. EDGEWORTH, M.D.

CUVIER published two figures in which the muscles connected with the jaw in *Orycteropus* are shown, but the scale is so small that the origins and insertions are not clear, and there is no accompanying text. A "Digastric" or "Digastrique" was described by Humphry, Macalister, and Chaine. Humphry and Chaine gave an account of the origin of the Stylohyoideus, and Bender<sup>1</sup> of its insertions into the C. branchiale i.

It seemed desirable to ascertain whether a Digastricus anterior, Pterygo-tympanicus, and Tensor veli palatini exist; and to determine the innervation of the "Digastric" and so make sure of its morphology.

This became possible by dissection of specimens kindly sent me by Dr Haagner, of Pretoria, and Dr Arnold, of Bulawayo.

The Temporalis arises chiefly from the Parietal and Squamous bones. Its origin extends forwards to the posterior margin of the Frontal bone, backwards on the superior surface of the Occipital, downwards to the Alisphenoid, and along the inner surface of the Zygomatic process of the Squamosum. The origin does not reach the mid-dorsal line. The upper part of the muscle is covered externally by fascia which is, ventrally, attached to the upper edge of the zygomatic arch. The muscle extends downwards and forwards, and is inserted to both surfaces of the coronoid process of the lower jaw, and to its anterior and posterior margins. The anterior surface of the upper part of the muscle forms the hinder border of the orbit. In the upper part of the muscle there is a cleft extending inwards and forwards from the external surface to the coronoid process, and separating the outer part of the muscle into anterior and posterior portions. The hinder edge of the anterior portion glides over a facet on the upper end of the coronoid process to which no muscle-fibres are inserted.

The Zygomatico-mandibularis, of vertical fibres, arises from the ventral edge of the zygomatic arch and, anteriorly, from its inner surface. It is inserted into the external surface of the lower jaw, above a slight ridge which extends downwards and forwards from the condyloid process. Its hinder portion is visible, externally, above the Masseter. The N. massetricus, passing outwards through the notch between the condyloid and coronoid processes of the lower jaw, sends two branches upwards into the posterior part of the Temporalis, and then passes forwards on the inner side of the Zygomatico-temporalis, giving branches to it, and then outwards to the Masseter. The muscle then

<sup>1</sup> Bender had only the excised pharynx and larynx at his disposal.

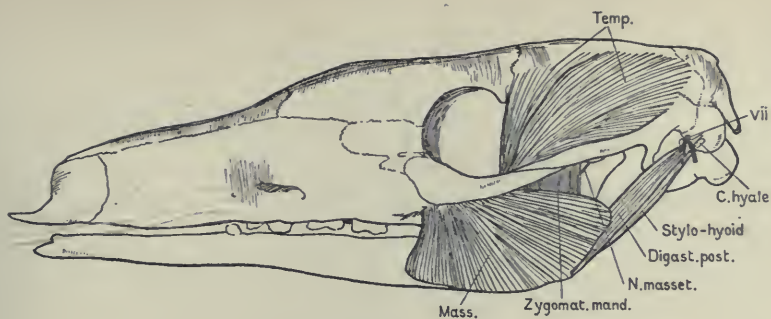


Fig. 1. Lateral aspect.

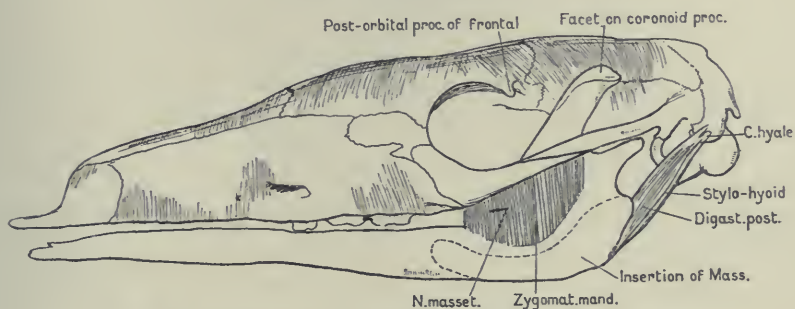


Fig. 2. Lateral aspect. Temporalis and Masseter removed.

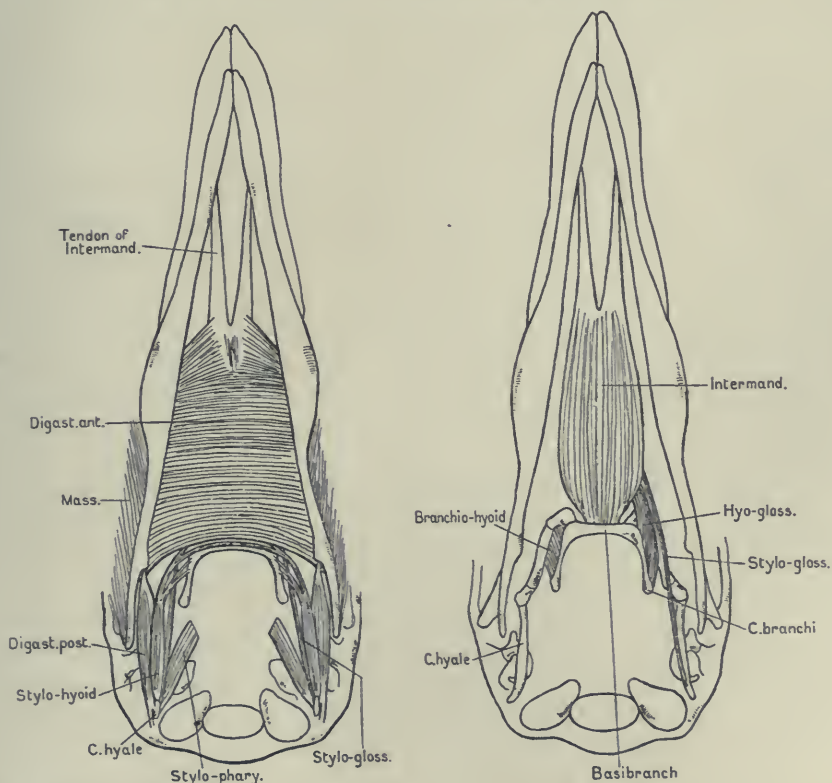


Fig. 3. Ventral aspect.

Fig. 4. Ventral aspect. The Digastrici anteriores have been removed, to expose the Intermandibularis. The Hyo-glossus has been removed on the right side, to expose the Branchio-hyoideus.



consists, in Schulman's terminology, of a Portio anterior and Portio posterior, but the division is shown only by the passage of the nerve. The Portio posterior is, internally, confluent with the Temporalis throughout its whole length, and the Portio anterior with it at its insertion.

The Masseter arises from the lower edge of the jugal portion of the Zygomatic arch. The fibres, covered by fascia, spread downwards and backwards fan-like to the external surface of the lower jaw, where it is inserted below the ridge passing downwards and forwards from the condyloid process. The most dorsal fibres lap round the neck of the condyloid process and join those of the Pterygoideus internus.

The Pterygoideus externus arises from the lower portion of the Alisphenoid in front of the alisphenoid foramen. It passes backwards and outwards and is inserted to the condyloid process of the lower jaw.

The Pterygoideus internus arises from the whole of the lateral surface of the Palate bone. Its origin extends, anteriorly, to the lower end of the orbital wing of the Frontal bone, and posteriorly, to the lateral surface of the Pterygoid bone—between the Pterygo-tympanicus below and the Pterygoideus externus above. It passes backwards and downwards and is inserted to the inner surface of the jaw below and behind the inferior dental foramen. Its upper margin wraps round the neck of the lower jaw just above the Processus angularis and joins the Masseter. The muscle is single at its origin; as it passes downwards it partially separates into three portions. The hindmost passes vertically downwards; the middle downwards and backwards, slightly overlapping the hindmost portion; the foremost passes backwards to the jaw, overlapping the other two portions. Both Pterygo-tympanicus and Tensor veli palatini exist, and together form a digastric muscle. The former arises from the lower edge of the Tympanicum, partly by means of a dense fascia. The fibres pass forwards and inwards, lying in a slight hollow on the outer side of the Pterygoid bone, from which some fibres arise. They converge to a tendon which passes forwards and inwards, in a cartilage-clad groove in the vertical ridge of the Pterygoid bone, into the soft palate where it expands into the Tensor veli palatini which passes inwards and forwards towards the middle line dorsal to the thick longitudinal muscle-stratum which forms the main bulk of the soft palate.

The Tensor tympani arises from the anterior limb of the ring-like Tympanicum and passes to the malleus.

The Genio-hyoideus arises from the lower edge of the jaw—behind the attachment of the Intermandibularis. It passes backwards as a flat muscle ventral to the Genio-glossus, to which it gives some fibres, joins its fellow and is inserted into the Basibranchiale and the median ends of the C. hyalia.

The Genio-glossus and the Genio-hyoideus are innervated by the XIIth.

The Intermandibularis is a median longitudinal muscle immediately ventral to the Genio-hyoidei. Its hind end is attached to the Basibranchiale. Its anterior end diverges right and left; each part converges to a thin flat

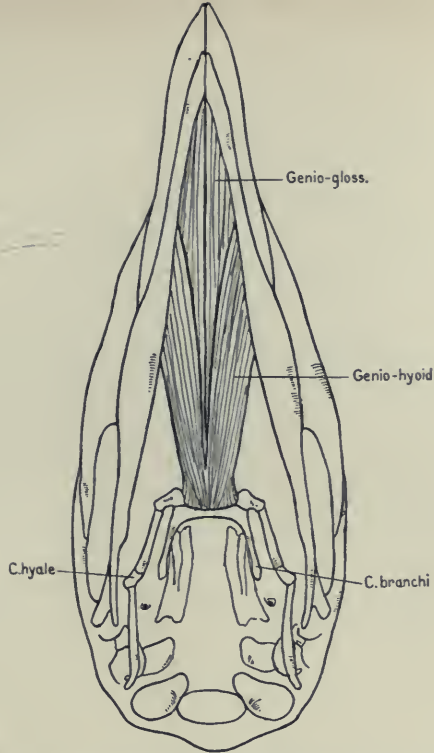


Fig. 5. Ventral aspect. The Digastrici anteriores and the Intermandibularis have been removed to expose the Genio-hyoidei.

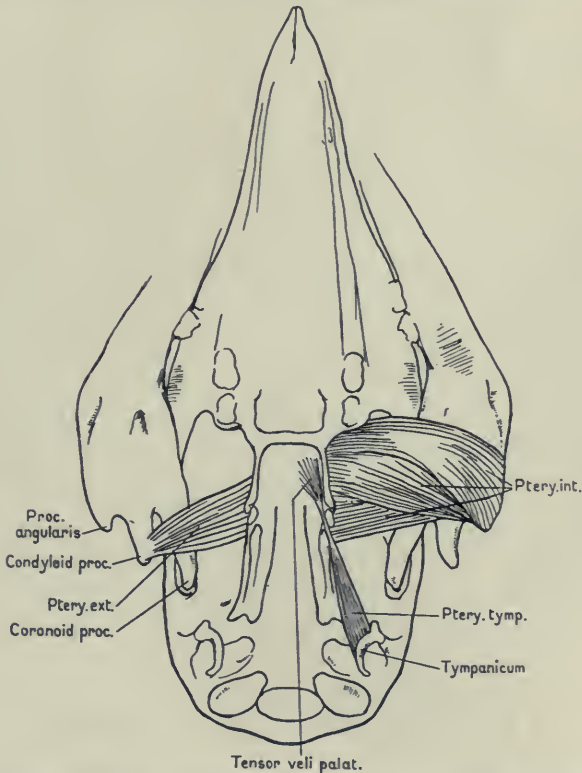


Fig. 6. Ventral aspect. The ventral edges of the jaws have been splayed outwards, to expose the Pterygoid muscles.

tendon which is inserted to the lower end of the jaw at a little distance behind the symphysis.

The two *Digastrici anteriores* form a thin sheet of transverse muscle fibres between the internal surface of the jaws<sup>1</sup>. There is a variable median raphé in the *Intermandibularis* and *Digastrici anteriores*. In one specimen (the one depicted) it was absent, in the other present, in both muscles. Some of the hinder fibres are continuous with the lower end of the *Temporalis*. The hindmost fibres are inserted just above the tendon of the *Digastricus posterior*, but there are no fibres, either muscular or tendinous, between the two muscles. The hinder edge of the muscle-sheet is concave. The anterior fibres curve a little forwards and end on the surface of the diverging anterior ends of the *Intermandibularis*. The *Intermandibularis* and *Digastricus anterior* are innervated by the R. mandibularis V.

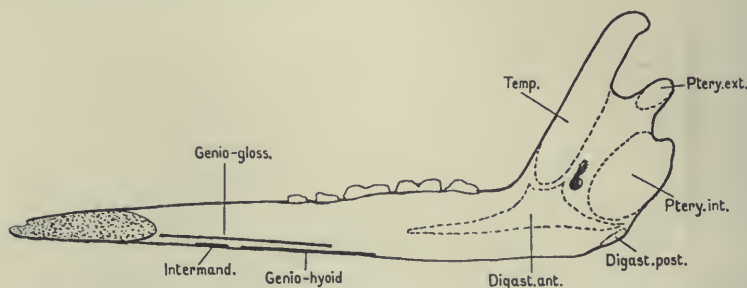


Fig. 7. Right jaw, inner aspect—showing the attachment of the muscles.

The *Digastricus posterior*<sup>2</sup> takes origin, fleshy, from the paroccipital process and, tendinous, from the upper end of the C. hyale. It passes downwards and forwards on the inner side of the jaw and tapers to a ligament which is inserted to a projection on the inner side of the angle of the jaw.

The *Stylohyoideus* takes origin from the upper end of the C. hyale and the tendinous part of the *Digastricus posterior*. It passes downwards and forwards and separates into two parts; one is inserted by two fasciculi into the C. branchiale i of the hyoid bone; the other passes on and turns inward just behind the posterior concave edge of the *Digastricus anterior* and meets its fellow in a median raphé. Some fibres join the posterior edge of the *Digastricus anterior*.

The *Digastricus posterior* and *Stylohyoideus* are innervated by the R. hyoideus VII.

#### COMMENTS

1. The *Pterygo-tympanicus* and *Tensor veli palatini* are both present, and together form a digastric type of muscle. In possessing both muscles *Orycteropus* resembles *Bradypus marmoratus* and *Choloepus* among *Xenarthra*, and *Manis*.

<sup>1</sup> Mylohyoïdien, of Cuvier.

<sup>2</sup> Digastrique or Digastric, of previous writers.



2. The innervation of the Digastricus posterior by the VIIth excludes the possibility of the muscle being a *Detrahes mandibulae*.

The two Digastrici anteriores form a sheet of transverse fibres between the jaws and are not connected with the Digastrici posteriores which are inserted into the angles of the jaws. The Stylohyoideus is inserted partly into the C. branchiale i and partly meets its fellow in a median intersection.

The condition of the Digastrici anteriores is thus as simple as in *Monotremes*, whilst that of the hyoid muscles is different from, and less primitive than, that existing in *Monotremes*, *Marsupials*, *Xenarthra*, and *Manidae*. In regard to these structures *Orycteropus* resembles the higher Mammalian orders—in which there is a Stylohyoideus, and a Digastricus posterior attached to the Digastricus anterior by intersection or tendon—but differs in that the Digastricus posterior is inserted into the jaw.

3. The Intermandibularis is a median longitudinal muscle, and acts as a protractor of the hyoid. This secondary condition, which is not present in any other Mammal, is perhaps related to the feeble development of the Geniohyoideus. The original transverse direction of its fibres is shown by those of the Digastrici anteriores, which have retained it.

I have the pleasure of thanking Dr Haagner and Dr Arnold for the specimens, and also Sir Arthur Keith for the loan of a skull.

The figures were drawn by Miss Cross.

The expenses were met by a grant made by the Colston Research Society.

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## AN ABNORMAL ATLAS

BY R. H. HUNTER, M.B.,

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THE abnormal atlas and axis which are described below were discovered in a collection of bones which were being classified for use in the department. Both bones are of average adult-size. They show no sign of disease and there is no indication that the condition they present might be the result of accident.

The condition is as follows. The odontoid process is separated from the axis and is incorporated in the atlas as its centrum. This body lies between the anterior parts of the lateral masses and is perfectly continuous with them, there being no markings on the surface which would indicate lines of fusion.



Fig. 1. The atlas viewed from above.

It is fused also with the anterior arch of the atlas, but the upper and lower edges of this bar can be traced easily from one side to the other across its anterior face<sup>1</sup>. Along the groove at the lower edge there are the remains of the attachment of the anterior common vertebral ligament. The lower surface of the atlas body is smaller than the upper surface of the body of the axis and does not fit well with it, though the two surfaces have a general slope from before backwards and downwards; and the indications are that an intervertebral disc lay between them. Across the lower part of the posterior face of the atlas body there is a smooth groove which would lodge the transverse ligament. Above this groove there is a rounded swelling and beyond this the bone tapers to a small upper articular surface. Whether this surface met the

<sup>1</sup> An X-ray photograph shows that while the centrum is denser than the other parts of the atlas, there are no cavities between it and them.

occipital bone or a separated apical odontoid element I am unable to say, since neither of these parts was found; but the flatness of the surface from side to side and its concavity from before backwards (fig. 1) would indicate, I think, a third occipital condyle.

So far as I have been able to discover this is a unique specimen, the nearest approach to it being a specimen in Professor Bolk's collection which he describes (in a letter to Professor Walmsley) as "a conrescence of the atlas with the occipital bone in which the odontoid process is fused with the anterior arch of the atlas. The axis belonging to this specimen is absent."



## EMBALMING IN THE TROPICS

By GORDON HARROWER, M.B.,

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THE preservation of bodies for anatomical dissection in the tropics is a somewhat more difficult matter than in the comparatively cold climate of the British Isles. Singapore is situated on a small island a few miles north of the Equatorial line. The temperature throughout the year is fairly constant round about 88° Fahrenheit in the shade, but the temperature is only maintained by rapid evaporation from the sea, and in consequence, the atmosphere is saturated with moisture. After sundown the moisture is precipitated from the atmosphere, and by contrast the air feels quite cold due to the vaso-motor system of the Tropical residents responding less readily to cold than residents in a cold country. The combination of warmth and moisture is ideal for the growth of mould, our greatest enemy in the anatomical rooms. So long as the skin is intact the body is comparatively safe, but as soon as the tissues are exposed the growth of mould is wonderfully rapid. I have seen a growth a quarter of an inch in thickness occurring in a single night. The common bluebottle finds the climate to its liking and within an hour of death swarms of them are busy depositing their eggs in the natural orifices of the body or any fold or crevice available. The eggs develop rapidly and the resulting larvae (maggots) bore through the skin or mucous membrane and set up decomposition with all its unpleasant odours. On my arrival in Singapore in April, 1922, the injection fluid in use was an arsenic mixture of the following formula:

Oxide of arsenic in powder	$\frac{1}{2}$ lb.
Carbonate of potash	... $\frac{1}{2}$ lb.
Water	... ... 4 pints

Boil till dissolved and add formalin  $1\frac{1}{2}$  pints and glycerine  $1\frac{1}{2}$  pints.

My first term in the Anatomy rooms was rather an unpleasant experience as the growth of mould caused the tissues to become soft, black, and rather sticky, not to mention odoriferous. The following term I commenced experimenting with injection fluids to prevent if possible the mould. At Glasgow University a mixture consisting of methylated spirits, carbolic acid and glycerine was used when I was Demonstrator there. I tried this mixture in Singapore, but the result was rather discouraging for before the end of the first week the body had to be buried on account of rapid decomposition. I tried many other fluids varying the amount of carbolic acid and formalin with the addition of zinc sulphate with varying degrees of success. Finally I evolved

the following formula which reduces the growth of mould to a negligible minimum:

Acid Carbol. (crystals)	$\frac{3}{4}$ lb.	
Methylated spirits	...	} of each 1½ pints
Glycerine	...	
Formalin	...	

In mixing this solution it is essential that the crystals be dissolved in the formalin before adding the spirits and glycerine otherwise solution is difficult. Heating the crystals in their container assists their solution. The total volume is small but the bodies are injected before the natural body fluid has time to evaporate. The spirit checks the corrosive action of the carbolic on the tissues and the hands of the dissectors, the glycerine retards evaporation and neutralises partly the hardening effect of the formalin.

When the arsenic mixture was used it required the combined strength of two or three men to flex the thigh to get the body in the lithotomy position for dissection of the perineum. The position was only attained by fracturing the vertebral column in the lumbar region or rupture of the muscles round the hip joint. By the glycerine carbolic method the joints are easily flexed.

No matter which injection fluid is used, in a climate like that of Singapore, it is essential that the bodies should be injected within a few hours of death. In twelve hours decomposition has commenced and progressed to a stage comparable to that in Glasgow of three to four days after death. After twenty-four hours the subject is quite useless for dissection purposes. While injecting it is important that the arms should be fully abducted otherwise there is a tendency for the lung capillaries to burst before the fluid has reached the extremities of the finger-tips due to the liability of the axillary artery to collapse in the adducted position of the limb.

As a colouring mass I use one pound of starch coloured with carmine made up to one and half pints with water and the addition of two ounces of formalin. The mass is injected hot and sets firm. A period of five days should elapse between the two injections. Formerly in Singapore a colouring mass of the following formula was used:

Red lead	...	$\frac{3}{4}$ lb.
Fat	...	$\frac{3}{4}$ lb.
Boiled linseed oil	12 ounces	
Oil of turpentine	10 ounces	

The mass was injected hot but as it never set firm, when a vessel was punctured, the mass oozed out and it became impossible to keep the dissection clean.

Finally, it is important that all natural orifices on the surface should be plugged with cotton-wool soaked in pure formalin to kill off any eggs which may have been deposited. If the body is washed over with oleum terebenthini or other cheap essential oil it keeps away flies and other insects and thus prevents the formation of maggots.

The dissection of the feet and hands offers some difficulty, as even in a saturated atmosphere desiccation is considerable. One method advocated about two years ago is to inject fluid under the skin by means of a syringe<sup>1</sup>. This method is quite satisfactory, but it is easier to remove the skin from the hand or foot at the beginning of the term and wrap the part in a cloth soaked in equal parts of glycerine and water to which a small quantity of preservative fluid is added. If the air is excluded by means of a covering of rubber tissue the part keeps quite soft. Even if the part has been allowed to dry after removal of the skin, soaking in water for twenty-four hours will render the part suitable for dissection.

<sup>1</sup> O. V. Batson: "Restoring mummified anatomical material," *Anatomical Record*, vol. 22, p. 165.



## RUDIMENTARY OTOCEPHALY

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DR FAUSTO LAGE sent me from the Island of Fogo (Cape Verde) the head of a human foetal monster. He informed me that, with the exception of the anomalous conditions of the head and the heart being partly displaced to the right side, no other anomaly was found. No further information relating to this specimen has been obtained. The brain was unfortunately destroyed.



Fig. 1. Represents the head of the monstrous foetus, the mouth of which is a small vertical median cleft.

The skin was brown in colour (No. 29 on the colour scale of the skin and the pilose system, according to the Instructions of the Société d'Anthropologie de Paris); the hair was black and curled and in colour approached to No. 48 of the aforesaid scale.

The head weighed 200 grammes. The mouth was the most remarkable feature, being reduced to a vertical cleft in the median line (fig. 1). The mouth cleft was 3 mm. high and .5 mm. wide and was surrounded by an ovoid mucous border 9 mm. high and 4 mm. wide. This mucous border represents

the lips, which are provided with but one commissure situated at the lower end of the cleft where the mucous border on either side comes to an end.

No vestige of a mandible could be found by palpation, there being nothing but soft parts below the level of the mouth. The ears appear to occupy a very low position, their lobules being on a level with the inferior plane of the face.

The following measurements were made:

Height of the nose	...	...	...	...	...	20 mm.
Breadth of the nose	...	...	...	...	...	17 "
Distance between the base of the nose and the upper end of the mouth	...	...	...	...	...	7 "
Breadth of the palpebral cleft	...	...	...	...	...	11 "
Distance between the internal angles of the two eyes	...	...	...	...	...	16 "
Length of the ear	...	...	...	...	...	29 "
Breadth of the ear	...	...	...	...	...	20 "
Distance between the two lobules	...	...	...	...	...	52 "

It was impossible to measure the diameters of the head, as the bones were dislocated.

On dissecting the specimen, the cavum oris was observed to be flattened and apparently destitute of a tongue (fig. 2). Two openings were found therein:

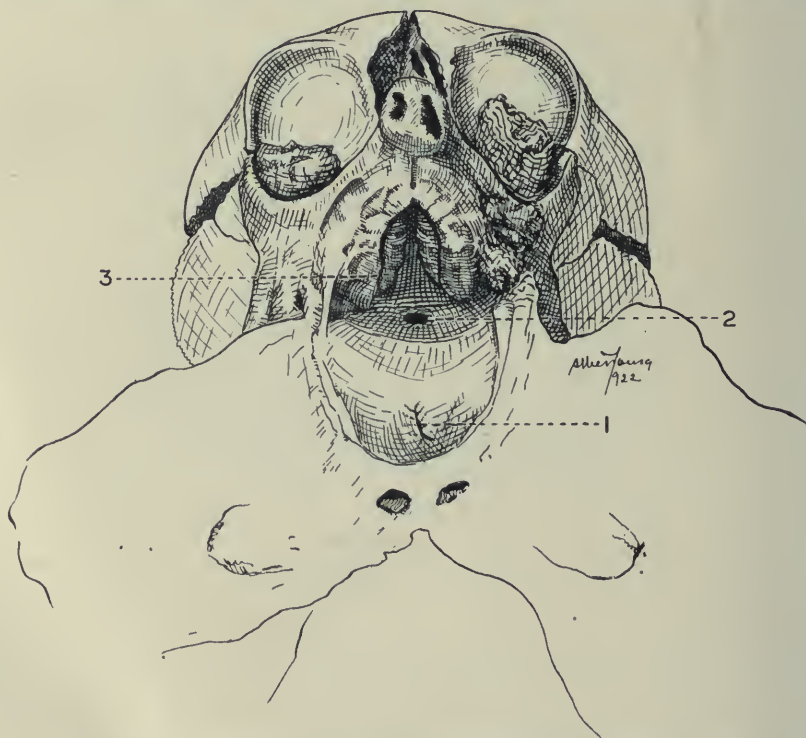


Fig. 2. The orbital and palatal regions of the head viewed from below and in front. The skin of the face has been reflected downwards, the palpebral apertures, nasal openings, and mouth opening (1) being seen on its deep aspect. The palate is interrupted by a single median cleft flanked by the palatal processes. The dental arch (3) is narrow, its sides being nearly parallel and approximated towards the median plane. Below the hinder part of the palate is seen the faucial opening (2).

an anterior (fig. 2. 1), the mouth in the form of a vertical cleft with fringed borders, and a posterior, an oval funnel-shaped opening 4 mm. wide (fig. 2. 2), representing the isthmus of the fauces.

The dental arches were lined with a festooned mucosa. Medial to the two dental arches and parallel with them two other arches were found (fig. 2. 3) on either side of a deep furrow representing the median line of the roof of the mouth. Between these protuberances and the dental arches other furrows, less deep than the median one, were seen. The maximum distance between the dental arches was 12 mm.



Fig. 3. Dissection of the basis of the head, in which the atrophied mandible (1), some subjacent muscular fascicles (2, 3), the rudimentary basis of the tongue (4) and the section of the oesophagus (5) are to be seen.

No vestibulum oris was present and the soft palate was reduced to a small fold with a free concave border.

On dissecting the neck a very much atrophied representative of the mandible was found. It was inserted below the cavum oris, in the formation of which it took no part (fig. 3. 1). It was greatly deformed and was closely applied to the base of the skull.

The symphysis mandibulae was only 20 mm. distant from the prevertebral region. Its anterior surface was very slightly convex, its inferior border was



everted, the condylar and coronoid processes were relatively long and almost horizontal. The angle of the jaw was absent and the differentiation between the body and the ramus was indistinct. The total length of this bone was 34 mm., each condyle measuring 6 mm. The height of the bone in the median line was 9 mm.

Several muscles (representing the styloid and digastric groups) were found below and behind the mandible; the fibres of two of these muscles (fig. 3. 2, 3) crossed the median line and were parallel to the inferior border of the bone. Behind these muscles a fleshy formation was lodged (fig. 3. 4) in a cavity, the posterior wall of which was formed by the anterior wall of the oesophagus (fig. 3. 5). I am of the opinion that this fleshy formation represented the root

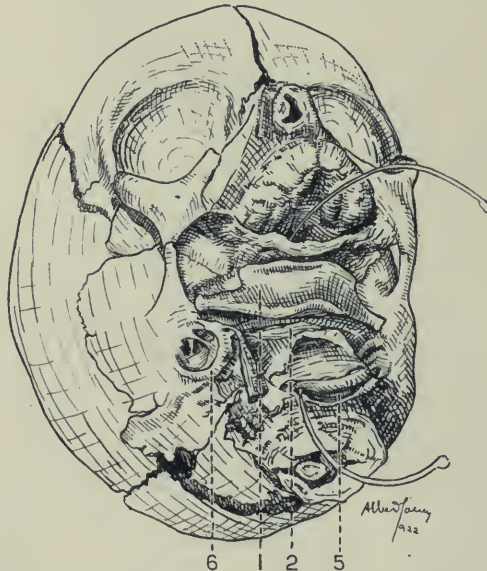


Fig. 4. Inferior and lateral faces of the dissected head, demonstrating: (1) the mandible, which does not take part in the formation of the buccal cavity, as may be verified by means of a stylet introduced into the oesophagus (5), and coming out of the mouth.

of the tongue. A seeker introduced into the oesophagus could be passed into the cavum oris, as is shown in fig. 4. The same figure demonstrates how completely the mandible was separated from the cavum oris.

Behind the isthmus faucium was a relatively small pharynx and in the median line the semblance of a broad and thin uvula was found. Two small choanae opened into the pharynx and on its walls were well developed pharyngeal openings of the two Eustachian tubes.

Unfortunately the dissection of the head left no trace of the larynx or of the hyoid apparatus. The pars tympanica (fig. 4. 6) was almost completely fused with the rest of the temporal bones and was separated from its fellow on the opposite side by a distance of 27 mm. only. The anterior tympanic spine was very well developed. The tympanic ossicles were normal.

The nasal bones were triangular with the base below. The two temporal bones were relatively close to one another and were provided with short and broad zygomatic processes. The fossae mandibulares were displaced downwards.

The sella-turcica was reduced in size and the dorsum sellae was still cartilaginous. The posterior clinoid process was united to the anterior by means of a fibrous cord, 3 mm. long on the right side and 2 mm. on the left.

When, by a teratogenic process in the embryo the two eyes are brought nearer to each other and atrophy of the higher part of the head takes place, a condition of monstrosity called cyclopia is produced; if on the other hand the ears are brought nearer to each other and a concomitant atrophy of the lower regions takes place, there results a condition which Isidore Geoffroy Saint-Hilaire<sup>(10)</sup> has termed otocephaly. In the group of the otocephalians he included five genera, the simplest of which is the Sphenocephalic, in which the two eyes are well separated but the two ears are close to one another and are united under the head, the mandible and the mouth being distinct. Only two of these specimens were recorded. I. G. Saint-Hilaire also mentions a twin monster heterodymus, in which the mouth of the parasite was imperforate.

The Sphenocephalic genus had been recognised by the father of I. G. Saint-Hilaire<sup>(2)</sup>. But before these taxonomic groups had been conceived monsters with the mouth and mandibles atrophied or completely missing had been recorded by several observers.

St Isidore of Seville<sup>(3)</sup> had noted certain monsters: "Aliis concreta ore esse, modico tantum foramine calamis venarum potum haurientes," while Ruysch<sup>(4)</sup> observed the foetus of a sheep without a vestige of a mouth.

Other authors, ancient and modern<sup>(5)</sup>, describe monsters, more or less similar to my case, giving them various designations. Indeed in the group of the Otocephalians of I. G. Saint-Hilaire the Hypomicrognathus and the Hypoagnathus, of Taruffi, the Nanocephalus brachygnathus and the Atretocephalus astomus, of Gurlt, etc., might be included. Taruffi cites some cases in which there was transposition of the viscera, as may have been the case with my specimen. He mentions further observations, recording, as in my case, atrophy of the mandible, a mouth reduced to a vertical cleft and a rudimentary tongue.

More recently, Nicolas and Prenant<sup>(6)</sup> have described the foetus of a sheep in which no mandible was to be found and the communication between the mouth and the nasal cavities, as well as that between the pharynx and the larynx were missing.

Lastly, Louis Blanc<sup>(7)</sup>, in a study of otocephaly occurring in 15 domestic animals has revised the whole question, and in creating three new genera has accepted the theory that this monstrosity is the result of a precocious stoppage in the development of the first pair of branchial arches.

In Blanc's series there are eight types of Otocephaly, the simplest of which is Agoniocephaly, characterised by: absence or rudimentary condition of the

mandible, occlusion of the isthmus faucium, presence of a pharyngeal sac, closeness of the middle ears, well formed skull and sense organs and the existence of a mouth.

My specimen obviously approaches this type, but it is still simpler, as the isthmus faucium is not completely closed.

As incipient forms of cyclopia have been recognised by Watkyn-Thomas (8) and myself (9, 10), conditions similar to the case now recorded may be regarded as exhibiting rudimentary otocephaly.

However, developmental perturbations of the branchial arches and clefts may be much simpler than in the present case. The same teratogenic process may result in agenesis of the external acoustic meatus and atrophy of the ears only. I am acquainted with six cases of this malformation, two I have already published (11, 12) and I hope soon to write a general survey of them all.

The absence of a tongue within the cavum oris and the existence of a lingual bud behind and below this cavity in the specimen now described, can be explained by embryology as it is well known that the anterior part of the tongue has not the same origin as its pharyngeal part (13).

This is not the first time that I have observed a similar disposition. In an otocephalic pig I dissected (14) (Blanc's Otocephalian sphenocephalic), both mouth and an independent tongue were absent, but the interior of the pharynx presented some mucous lingual rudiments.

In short, the monstrous head I have described is a case of tendency to otocephaly and approaches Blanc's type Agoniocephaly (Bujard's Agnathy (15)). Its most striking features are: the buccal cleft which has a vertical direction; the atrophy of the mandible and its displacement downwards and backwards relatively to the cavum oris; the lack of a tongue within that cavity; the absence of a vestibulum oris; the stenosis of the isthmus faucium and the approximation of the external and middle ears of the two sides.

In my opinion, this monstrosity is closely related to the cases of agenesis of the external acoustic meatus, which are sometimes complicated with atrophy of the mandible and are, so to speak, the first step of a developmental perturbation, which, were it more profound, would lead to otocephaly.

My best thanks are due to my assistant, Dr Alberto de Souza, for the drawings.

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# NERVE ENDINGS IN MUSCLES

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(Plates I—IV)

## I. INTRODUCTION.

STATEMENT OF FACTS AND VIEWS MORE OR LESS PRECISELY ESTABLISHED.

(a) *Motor-nerve termination in striated muscle fibres.* The small medullated nerve stem, on entering the striated muscle, little by little splits into separate fibres the number of which considerably increases owing to repeated dichotomous division.

All the fibres lie in the interstitial connective tissue (perimysium internum), where between the nerve bundles are very frequently found transverse and oblique anastomoses so that to a certain extent it is possible to recognise in the muscle the existence of nerve plexuses. The branches of this plexus in the shape of medullated nerve fibres approach the muscle fibres and terminate in them, often dividing into two or three small branches.

According to the predominating opinion, at the place of entrance into the muscle fibre, the sheath of Schwann joins with the sarcolemma, the nerve fibre loses its medullary sheath but the axis cylinder passes inside and, ramifying, places itself *immediately under the sarcolemma* in the isotropic substance of the muscle fibre.

All these statements concern vertebrate animals and according to the work of many investigators (Rouget, Kuhne, Ranvier and others) are definitely established. There are only a few investigators (Krause, Kölliker) according to whom the axis cylinder does not enter the muscle fibre but places itself on its surface. Nevertheless, in spite of the very authoritative names of the last named authors, their opinion, in view of a great number of observations, which prove that the axis cylinder passes *through the sarcolemma* cannot be sustained. As to the further relations of the axis cylinder inside the muscle fibre, they may be different in different animals and from very exact data we may accept two types of nerve endings: (A) *in the shape of terminal plates of Rouget*, and (B) *in the shape of Kuhne's bundles*.

(A) *Terminal nerve plates of Rouget.* Every nerve plate consists of two parts: (1) *the ramification of the axis cylinder*, and (2) *the finely granular substance of the so-called granular lining of Kuhne*. The axis cylinder in the terminal plates divides into a very large number of branches, which have an

irregular shape; in some places they thicken, in others on the contrary they become as fine as the thinnest filament.

All these ramifications lie immediately under the sarcolemma on the granular *lining*, into the thickness of which they perhaps do not penetrate and, consequently, are not in immediate touch with the contractile substance of the muscular fibre. There are cases in which a thin filament separates itself from the terminal plate, leaves the given muscular fibre and terminates in another (Perroncito).

As to the granular lining of the nerve plate, our knowledge concerning its structure and especially its designation is still very insufficient. It is very possible that here we are dealing with a more or less considerable accumulation of sarcoplasm of the muscular fibre. This is all the more credible because in the terminal plates a large number of nuclei may also be seen. These latter Ranvier divides in this way: (1) nuclei of the granular substance (noyaux fondamentaux), (2) nuclei, belonging to the ramifications of the nerve (n. de l'arborisation), and (3) nuclei of the sheath of Schwann covering the terminal plate (n. vaginaux).

The terminations of nerve fibres in the shape of terminal plates characterise the reptiles, birds and the mammalia.

(B) In the frogs and generally in the amphibia the nerve terminations of the second kind are found *in the shape of Kuhne's terminal bundles*. In this case the axis cylinder after passing through the sarcolemma, ramifies as in the plates, but these ramifications appear in the shape of long thin threads, running under the sarcolemma in most cases along the muscular fibre and seldom at an angle.

The terminal filaments appear to be of even-calibre or moniliform (Tchiriev). Along their extent nuclei are met with, to which Kuhne attributed special importance and called them *terminal buds*. However, this interpretation has not been accepted. In all probability these nuclei belong to the muscular substance. In this kind of nerve termination there is absolutely no granular lining, so that the terminal threads lie immediately in the isotropic substance of the muscle fibre. They never penetrate, however, into the depth of this latter, but end in attenuated or sometimes thickened terminations.

From the foregoing we see that the nerve fibre, although closely associated with the muscular fibre, has with it no organic connection.

(b) *Termination of the motor nerve in smooth muscle*. The nerve fibres which run into smooth muscle, form several plexuses. Klebs, to whom we are indebted for an exact description of the course of nerve fibres in smooth musculature, describes three nerve plexuses: (1) *fundamental*, consisting partly of medullated nerve fibres and still lying outside the muscular layer, (2) *interstitial or intermediary*, consisting of non-medullated fibres and lying between the muscular bundles, and (3) the *intramuscular* also of non-medullated fibres situated between the separate muscle cells.

At the present time it is possible to state with great certainty that the



terminal threads of the intramuscular plexus terminate on the surface of the part of the smooth fibre which contains the nucleus by a simple method of spreading and which Ranvier called the motor point (*tache motrice*). It is necessary to remark, however, that this kind of termination is strictly proven only for some invertebrates—namely for smooth muscles of the leech (Ranvier, Hanzen). For vertebrate animals this arrangement is not quite confirmed, but may be considered very probable, as shown by the investigations of Gscheidlen and Loevit.

Recent observations show that the finest nerve fibres penetrate between the separate muscle cells, touching them without any enlargements on their terminations (Arnstein, Retzius), or encircling the muscle cell by moniliform terminal threads (Agababoff, Timofeieff).

(c) *Termination of the nerve in connective tissue.* Recently it has been shown with certainty that in the connective tissue the nerve fibres may terminate in the same way as has long been accepted for the epithelia. In different kinds of connective tissue (fascias, synovial membranes, membranes of brain, tendons, etc.) a considerable number of separate forms of nerve terminations have been discovered which, however, may be divided into two groups:

(1) *Terminal meshes.* In a certain place the nerve fibre loses its medullated substance and for some time runs in connective tissue in the form of an axis cylinder, deprived of its sheath. This terminal nerve thread divides several times, and between the dividing fibres numerous anastomoses are formed and, finally, a mesh of the finest nerve filaments arises which constitutes the termination of the given nerve fibre (Nicholadoni, Ivanoff, Janchick and others). Further, in describing the nerve termination in the cornea of the eye, rather in its “stratum proprium,” we shall consider an example of a terminal mesh and will illustrate it.

The terminal network may be combined with free terminations, i.e. finest moniliform filaments may leave the terminal mesh and terminate freely.

(2) *Free terminations.* In connective tissue formations there exist, without doubt, also free terminations of the nerve fibre. Usually they present the following relations. The medullated nerve fibre in one place or another loses its medullary sheath and then runs in the connective tissue as a naked axis cylinder which terminates with free terminal ramifications. These latter vary very greatly in appearance; usually they appear either in the shape of little bushes of short threads, or as a brush-like or arborescent formation, etc. It is better to say—the terminal ramifications, identical in substance, submit with great difficulty to description in every individual case.

Out of all these forms it is, however, possible to recognise the *sensory plates* described by Smirnoff, which he found in the endocardium, and which were afterwards described by A. Dogiel in the walls of the blood vessels. The plates of Smirnoff also represent the terminal ramifications of the sensory nerve fibres in the form of short threads, always terminating with enlarged ends. In this respect they differ very slightly from other free terminations of the nerve in

connective tissue, but, nevertheless, they also have their characteristic peculiarity—namely, the ramifications of the axis cylinder rest on a plate of granular substance, similar to that in the motor plates of striated muscle fibres.

(d) *Nerve terminations in tendon.* Experimental investigations (Kattaneo) show that the nerve terminations in tendons belong to sensory nerves.

In their simplest form they fully correspond to the free terminations already described in connective tissue. The medullated nerve fibre, on approaching the place of termination in tendon, loses its medullary sheath and the naked axis cylinder penetrates between the secondary bundles, possibly divides several times and in the end terminates by more or less rich terminal ramifications. In Amphibia, the terminal ramifications bear the character of long threads stretching along the tendon bundles.

In mammals and man, the nerve terminations in tendons are, in substance, constructed in the same way, but differ in their external appearance. At the site of their disposition, usually at the transition of the muscle into tendon, part of this latter represents a spindle-like swelling. Several names have been given by the authors to these terminations—*tendon spindle* (Kölliker) or *muscle-tendon organ* (Golgi).

The nerve terminations in tendon of the Mammalia were quite precisely described by Golgi. They are also called in honour of this scientist—*corpuscles of Golgi*.

The nerve fibre, on approaching such a corpuscle enters into it, preserving the character of a medullated fibre. The membrane of Henle at this time becomes continuous with the membrane of Golgi's corpuscle. Inside this latter the nerve fibre subsequently divides two or three times, i.e. into branches of the second and third order, and only then loses its medullation. The naked axis cylinders appear already as terminal branches, which at a more or less considerable distance from their origin, divide into terminal ramifications in the shape of beautiful bushes of meshes wherein the free filaments terminate in most cases by definite swellings.

The sensory terminations in one form or another are proper to all tendons and are found not only in the region of attachment of the muscle to the tendon, but along all the course of the tendon (Ciaccio). In all probability the terminations in tendons are identical in substance with the nerve terminations in fascias and other connective tissue membranes (Ivanoff). To this same category of nerve terminations it may be necessary to add the *corpuscles of Ruffini*, which are found in the skin of the fingers, in the deep layers of "corium" and even in the subcutaneous cellular tissue.

The corpuscles of Ruffini have an oval shape, in size they attain 1.35 mm. and they are clothed in a compact membrane. The relations of the nerve fibre to this corpuscle are exactly the same as in the tendon spindles of Golgi.

(e) *Terminations of sensory nerve in striated muscles.* The sensory nerves terminate in striated muscles chiefly by characteristic formations known under the name of *muscle spindles* or *Weismann's bundles*. As is known, the muscle

spindle consists of a small group of thin muscular fibres enclosed in a connective tissue capsule. Such a muscle spindle is in relation with one or more medullated nerve fibres. Having passed the membrane of the spindle, the nerve fibres divide repeatedly, then lose their medullary substance and their terminal branches immediately pass into contact with the muscle fibres of the spindle, their terminations on the fibres presenting very different forms and so being difficult to classify under any definite scheme.

According to Polumordvinoff's observations the most constant appear to be two forms: (a) the axis cylinders acquire the shape of a *ribbon*, which *spirally embraces the muscle fibre of the spindle* and (b) the axis cylinders stretch along the muscle fibre and on their way give off a great number of short sprouts, each of which ends in a *wide leaf-like expansion*. The terminal ramifications of the axis cylinder end in the same way as the side branches. This second form may present a considerable number of variations.

Muscle spindles are not found in every muscle. There are evidently none in the muscles of facial expression, nor in the muscles of the mouth, throat and some other regions.

Independently of the nerve terminations in muscle bundles a certain number of sensory nerves are situated in the connective tissue layers of the muscle. According to Kölliker, these fibres terminate almost exclusively in the perimysium externum in the shape of long thin threads. Sometimes these latter pass into small plate-like expansions, from which run a small number of short moniliform threads (Polumordvinoff).

The free terminations of nerve fibres were observed by Timofeieff in the substance of the cremaster muscle. Here they appear sometimes in the shape of long moniliform threads, ending in button-like expansions. In other cases it is possible to see that the nerve fibre, after losing its medullated substance, divides into short little branches, which finally take on the appearance of cogged plates. Such a terminal apparatus is very extensive, embracing five or more muscle fibres lying side by side.

In addition to the above mentioned nerve terminations in striate muscle fibres of the amphibia, there are nerve terminations of a second kind very characteristic and exceptionally interesting. We find them displayed most plainly in snakes. They were first described by Tchiriev many years ago (in 1879) (*Tropidonotus natrix*) under the name of "terminaisons en grappes."

Tchiriev came to the conclusion that these terminations are only the young forms of the usual terminal or motor end-plates, that they are only found in undeveloped muscular fibres and that on attaining full maturity they become typical terminations of the motor nerve fibres.

With such an interpretation the "terminaisons en grappes" could not arouse any very great interest and were subject to very little serious examination by succeeding investigators. However, a very important circumstance did not escape some observers, including Tchiriev, namely that the "terminaisons en grappes" are associated with a non-medullated fibre, while the



motor termination is always associated with a medullated fibre which usually approaches the muscle fibre preserving its medullary sheath right up to the place of its termination, or only losing it at quite a short distance from the same.

This substantial distinction of the "terminaisons en grappes" from the usually accepted motor terminations gradually diminishes, according to Tchiriev and others, when the young muscle fibres attain full maturity and the "terminaisons en grappes" become the usual forms of motor terminations.

Those investigators who regard both forms of terminations as identical in substance fail to see any difference between them in other respects. Tchiriev and others definitely state, that both forms are identically related to the muscle fibre, in so far as both lie immediately under its sarcolemma (hypolemmal).

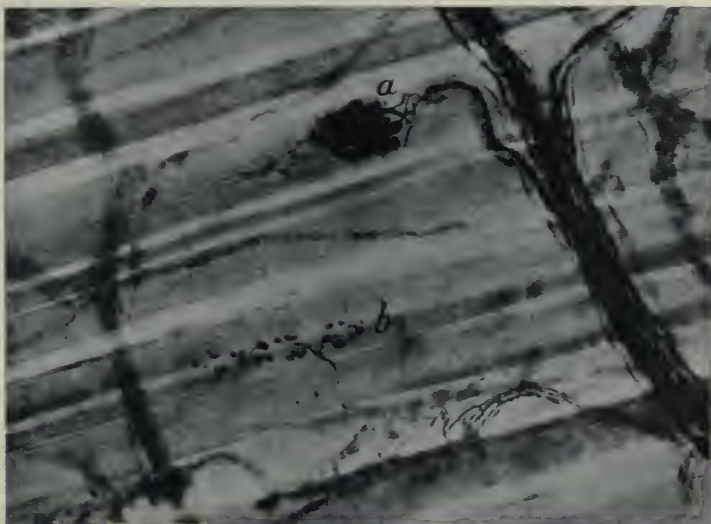


Fig. 1. Two kinds of motor plates: *a*—type I, *b*—type II. Python.

In the same way Tchiriev and others affirm that the "terminaisons en grappes" are supplied with finely granular substance on which lies the ramification of the axis cylinder. However, they affirm this with a certain proviso, acknowledging, that this does not always happen and that cases exist when terminations of this kind are devoid of finely granular substance, i.e. lack a substantial part of the usual motor terminal apparatus.

Tchiriev and his followers further hold that between the usual terminations of the motor nerve and the "terminaisons en grappes" there are transitional forms. Thus everything seems to point to the conclusion that in the muscles of *Tropidonotus* in spite of the apparent existence of two forms of nerve terminations, we are dealing only with one and the same form, the so-called "terminaisons en grappes" being merely an embryonic form of the first.

Most investigators have accepted this interpretation. Nevertheless Bremer (1883) who published, for his time, an excellent work, rightly says that although

it is possible to meet forms of "terminaisons en grappes" which appear to be transitional forms to the usual motor plates, still the difference between them is so great that both forms should be recognised as terminations "sui generis."

These differences will be pointed out later in the description of my preparations. The investigators who accepted the "terminaisons en grappes" as an independent kind of nerve termination, ascribed to them different functions, Bremer regarding them as motor, Giacommi as sensory nerve endings.

## II. PERSONAL INVESTIGATIONS OF NERVE TERMINATIONS IN THE STRIATED MUSCLES OF PYTHON.

Muscles of snakes served as material for my observations. I had at my disposal several kinds of snake, but I chiefly investigated the nerve terminations in the muscles of Python, utilising gold chloride according to Ranvier's method.

In the muscles of Python the nerves, approaching the muscle fibres, as in other animals, often divide before entering the muscle fibre, and then terminate in the so-called terminal plates. As Tchiriev's observations, referred to above, showed, there are two types of terminal plates in the muscles of snakes: (a) motor end plates, and (b) the so-called grape-like plates or the "terminaisons en grappes" (fig. 1, Plate-figs. 7, 8 and 9).

(a) The motor end plates, the structure of which is well known, present in the snakes the usual arrangement—the nerve-fibre passes towards the muscle substance through the sarcolemma, its axis cylinder loses its medullary sheath and divides into thin filaments, which end upon the finely granular lining (sole—according to German authors), supplied with nuclei (noyaux fondamentaux, Ranvier)—in short, it exhibits the same arrangement as in fish, lizards and mammalia.

The ramifications of the axis cylinder, however, present here certain peculiarities, not really substantial, but not without interest. The axis cylinder of the terminal nerve fibre, as we said, passes through the sarcolemma and its ramifications spread over a small area which is usually of a round or oval shape. There is hardly any doubt, that these ramifications lie immediately under the sarcolemma, but of course partially, if not wholly, immersed in the granular substance.

They have, as it appears, no relation whatever to the nuclei of this latter.

The ramifications of the axis cylinder in the form of very thin filaments either branch dichotomously—which seems to characterise the majority of collateral branches, or they branch irregularly or both forms of division are mixed.

But in all cases every filament finally terminates with characteristic enlargements, (fig. 2) representing either the thickening of the axis cylinder, or the accumulation on its end of some



Fig. 2. Motor plate (type I). *a*—axis cylinder, *b*—collateral. Python.

substance possessing considerable reducing capacity. In gold chloride preparations, if the reduction was successful, these enlargements of the axis cylinders are black, whereas the axis cylinders in the majority of cases are stained reddish violet or dark violet.

The motor end plate is also often approached by the collaterals of the nerve fibre belonging to it. They can participate in the structure of the motor plate, but sometimes turn aside from it and terminate in independent small motor plates, also under the sarcolemma.

There are cases when the collateral of the nerve fibre forms its own little additional plate. I present several figures made from microphotographs which may make the reader better acquainted with the structure of this kind of nerve termination, than a lengthy description (figs. 3, 4).

I think it necessary, however, to add, that besides the above described parts, i.e. the ramifications of the axis cylinder and the granular substance with its



Fig. 3. Motor plate (type I). *a*—axis cylinder, *b*—collateral. Python.



Fig. 4. Motor plate (type I). *a*—axis cylinder, *b*—collateral. Python.

nuclei, I could not observe any other system of fibres and think, that in snakes, they do not exist.

However, I must make a reservation. The expressed opinion is the result of my present observations, carried out with the aid of gold chloride. From this point of view they may appear to be somewhat onesided. I intend, however, at some future time to subject them to the necessary control, especially by means of Bielschowsky's method to which histologists attribute great importance.

I pass now to the description of plates of the 2nd type, "terminaisons en grappes" (fig. 5, Plate-figs. 7, 8 and 9).

The plates of the 2nd type are the terminations of non-medullated fibres. These latter, as usual, form before their terminations, extensive plexuses and then separating themselves in the shape of more or less considerable bundles direct themselves towards the muscle fibres and finally end in their characteristic terminations, whilst the medullated fibres always give one plate to each



muscle fibre. I, in common with other authors, must emphasise that *the medullated and non-medullated fibres never terminate in the same muscle fibre*. On the contrary a particular muscle fibre *always* receives either a medullated nerve with its plate of the 1st type or a non-medullated fibre with its plate of the 2nd type.

All investigators unanimously agree, that the terminations of the 2nd type have not the granular substance which is so characteristic for terminations of the 1st type. Then again the position itself of the 2nd type of plate is somewhat different from that of the 1st type.

If it be accepted that the plates of the 1st type lie under the sarcolemma (hypolemmally), this cannot be said about the plates of the 2nd type. On the contrary in the preparations, where the plate can be seen in profile it is readily seen that it lies outside the sarcolemma (epilemmally). If it is so, it will become clear why the plates of the 2nd type have no granular substance as this latter only represents an accumulation of the sarcoplasm of the muscle fibre and certainly lies inside the sarcolemma.

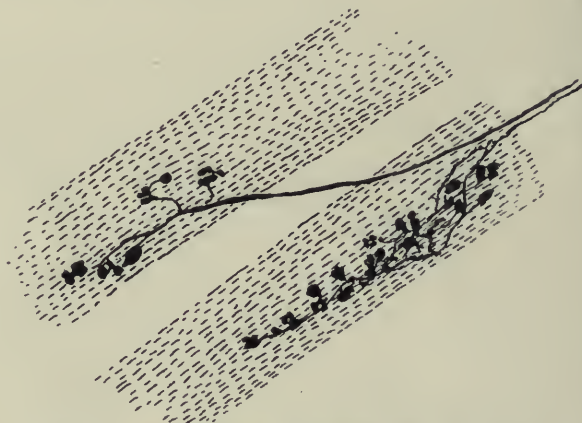


Fig. 5. Plates of type II, large and small. Python.

As to the shape of the plates of the 2nd type—it varies, but the elongated form predominates as we see in fig. 5 and Plate I, fig. 7.

A non-medullated fibre, on approaching the muscle fibre sometimes divides dichotomously like the medullated fibre and gives apparently two plates to one fibre. It is often possible to see that near its termination the bundle of non-medullated fibres forms a plexus, from which are given off either separate fibres or oftener thin bundles of fibres, which end on the muscle fibres with their characteristic terminations.

As we have said, the plate of the 2nd type often has an elongated shape. The nerve fibre or the bundle of fibres divides into its terminal filaments, which in their turn give out side sprouts and finally each terminal filament terminates with button-like enlargements. It is evident that the relations of the axis

cylinder also in these terminations are, in principle, the same as in plates of the 1st type.

*Ultra-terminal fibres.* Under this name are understood certain non-medullated nerve fibres, which sprout from the terminal ramifications of the axis cylinder of a motor plate, abandon the given muscle fibre and terminate in another neighbouring muscle fibre forming in it either a fully developed motor plate or a termination of a rudimentary form (Ruffini, Perroncito).

In other cases the terminal nerve filament does not stop in the second plate, but comes out of it again and then runs in the shape of a smooth thin fibre for a great distance, but the place and method of its termination have not yet been successfully defined.

The observations of Ruffini have obtained confirmation only in part. It was Perroncito who pointed out that the fibres, observed by Ruffini, might be seen without difficulty in the muscles of all animals. But Perroncito has also stated perfectly correctly that in the majority of cases these fibres appear to be only collaterals of motor fibres, terminating in the given muscular fibre. As was pointed out above and as is sufficiently correctly established at the present time, the motor nerve fibre on approaching the muscle fibre often divides two or three times, then loses its medullary sheath and already in the form of one or several non-medullated filaments enters the muscular fibre and terminates immediately under the sarcolemma in the so-called terminal plates or bunches according to the animal examined. Perroncito points out that Ruffini's fibres in the form of non-medullated moniliform filaments may sprout from the axis cylinders of motor fibres as their collaterals and either enter into the same muscle fibre, or may be, into a neighbouring fibre in which they terminate, forming in some cases small rudimentary terminal plates. Usually, they only terminate in button-like expansions.

Perroncito does not deny the possibility of Ruffini's case, i.e. he allows that the first filament may sprout not only from the axis cylinder of a motor fibre, but also from the axis cylinder ramification already in the motor plate itself.

Ruffini's statement, however, that his ultraterminal fibres pass through secondary plates and continue further, is not confirmed by Perroncito. The majority of investigators evidently accept Perroncito's conclusions (Crevatin, Fusari, Sommariva, Tello, Boeke and others).

With reference to my personal observations and my personal opinion about the ultraterminal fibre, or fibre of Ruffini, I consider correct the already firmly established opinion expressed for the first time by Perroncito, that the ultraterminal fibres, in the majority of cases are collaterals of the motor nerve axis cylinder.

However, I must make an addition as my observations somewhat differ from those of Perroncito and others.

According to my observations, the collateral sprouting from the axis cylinder before its entry into the muscle fibre, may in rare cases direct itself towards one of the neighbouring fibres, but in the majority of cases the collateral

accompanies its nerve fibre, enters the same muscle fibre and after passing through the sarcolemma either takes part in the construction of the terminal apparatus or turning somewhat aside, terminates independently, sometimes in the form of a small—as it were—additional plate.

As a result of my observations, I affirm that *the collaterals, having once penetrated into the muscle fibre, never leave it and never come out of its limits*. All the more I fail to agree with the observations of Ruffini and Perroncito that ultraterminal fibres may sprout from the axis cylinder ramifications already in the terminal plate itself and that they afterwards pass in the form of a non-medullated fibril into another muscle fibre. In my opinion the correct relations are described and represented by Perroncito in fig. 6 of his 1902 work. Figs. 2 and 4 of his work of 1901 may be very near reality, but allow of a different interpretation, i.e. they may represent collaterals of an axis cylinder which had not yet penetrated into the muscle fibre.

With comparatively small magnification, on examining the terminal plates from above or from below, it is exceedingly difficult to establish the place of departure of the thin filament and it is very easy even for an experienced observer to be deceived.

To illustrate my conception I present a microphotograph of one of my preparations. The drawing represents at "a" a nerve fibre terminating in a motor plate; the medullated nerve fibre, entering the terminal plate gives off one dichotomously dividing collateral, which together with its nerve fibre approaches the terminal plate and apparently participates in its structure (fig. 1).

The photograph also shows quite clearly that on the opposite side there branches off from the terminal plate a thin moniliform filament, terminating with small ramifications. This is, it appears, one of the cases in which the plate evidently gives off the so-called ultraterminal fibre. However, a detailed and careful study of these relations established beyond doubt that this interpretation is erroneous, and that in this case the so-called ultraterminal fibre does not branch off from the ramifications of the axis cylinder of the motor nerve fibre, but appears to be in reality only a collateral, which does not even pass through the plate, but passes over it, in close contact with its granular foundation.

And in all cases, when I had to investigate such areas in my preparations, when the branching off from the plate seemed almost beyond doubt, I could establish without fail, that these ultraterminal fibres represent continuations of the collaterals of the motor nerve fibre. It is interesting that the authors (Perroncito, Boeke) who formerly confirmed the existence of ultraterminal fibres as normal, at the present time consider them as only rare exceptions. I have observed no other fibres entering into connection with the motor nerve terminations in the muscles of snakes.

I must remark, however, that in one respect the observations of Ruffini are absolutely correct and in my opinion exceptionally interesting. Ruffini



observed a whole series of thin non-medullated nerve fibres, stretching for a long distance and presenting no moniliform enlargements. The place and method of termination of these filaments Ruffini unfortunately could not state. These fibres in very large numbers may easily be seen in the muscles of snakes.

I could demonstrate them on almost every one of my preparations but these fibres have another source and as we shall see presently, cannot be ascribed to the ultraterminal fibres.

It seems to me that these fibres should be attributed to those non-medullated nerve filaments, which were described long ago for the first time by Reichert and Kölliker and afterwards by Odenius, Sachs, Tchiriew and others.



Fig. 6. Nerve fibres in the intramuscular connective tissue. Python.

Not one of these authors gives any precise indication concerning these fibres, and not one establishes either their origin or termination. As we have just pointed out, Ruffini too, who has evidently observed these fibres, did not attribute to them the significance which they have in reality. I shall try to elucidate this question as much as I can with my own observations. In my preparations I could observe a large number of non-medullated fibres. They can run together with the medullated fibres, forming mixed nerve bundles but often join into independent bundles of non-medullated fibres.

In my Plate-figs. 7, 8, and 9 it is not difficult to see how from the mixed nerve stem, a side branch comes off composed of one medullated fibre and a bunch of

non-medullated fibres. The medullated fibre terminates in the usual motor plate and the bundle of non-medullated fibres divides into two parts, of which one ends in a terminal plate of the 2nd type and the other continues between the muscle fibres in the interstitial connective tissue.

If we follow this fibre, as far as possible, we are easily convinced that it divides into separate non-moniliform filaments which ramify or give out side branches and then terminate in the connective tissue with free terminations (fig. 6). These terminations may be easily observed by their appearance—they always acquire a characteristic appearance of short branching moniliform filaments.

To conclude the description of these non-medullated fibres, I must touch upon the question of whether these fibres are connected with the nerves of the blood vessels, the plexus of which, sometimes very extensive, we observe in the same layers of the interstitial connective tissue. Perroncito, at least, affirms this and just because of this ascribes the non-medullated fibres to the sympathetic system.

May be this is so, although personally I cannot say this with sufficient certainty. In examining my preparations I tried to solve this very essential question, but I never succeeded in establishing an indisputable relation between these nerve fibres and the nerves of the blood vessels.

Without denying the possibility of such a relation, I still regard it as doubtful.

#### MUSCLE SPINDLES IN SNAKES

These interesting and as yet enigmatic formations are constructed in principle in the same way in snakes as in other vertebrates.

According to the established opinion, each muscle spindle is unifascicular, i.e. is provided with only one fine muscle fibre. In muscles of snakes, as well as in other animals, two kinds of spindles are found, of which one presents a simple structure and the other a more complicated one.

The first kind is called "small muscle spindle" (*fuseau à terminaison circonscrite*, according to French authors), and the second "large muscle spindle" (*fuseau à terminaison étendue*—French authors). The majority of authors accept the somewhat astonishing peculiarity of the simple muscle spindles—namely, that the muscle fibre—along the extension of the spindle-like enlargements, in the place where the nerve-fibres enter the spindle—loses its cross striation, which in this place is replaced by the granular protoplasm (*sarcoplasma*).

The muscle fibres of complicated spindles preserve their usual structure and their cross-striation.

To these established opinions, I must add a correction in two respects. According to my observations the muscle spindles in snakes are not always unifascicular. Among them are found some that contain two fine muscle fibres (Plate IV, fig. 10) but no more. At least I have not met any spindles with more than two muscle fibres. As to the disappearance of cross-striation in muscle fibres of simple muscle spindles, it seems to me that here there is only a mis-

understanding. I have investigated this question carefully and have come to the conclusion that the muscle fibre of every spindle, the simple as well as the compound, on passing through the point of entry of the nerve, does not undergo any serious change in its structure and in all cases preserves its cross-striation (Plate IV, fig. 11). It is true that at the nerve ending there may accumulate, as in other cases, a large quantity of sarcoplasm and a large number of nuclei, but nothing more. Neither the thickness of the muscle fibre, nor its structure changes, according to my observations.

From the time of Ramon y Cajal and Kerschner's investigations (1888) the opinion has become established that the muscle fibre is supplied by both motor and sensory fibres. The investigations of the above mentioned authors were confirmed and completed by many further investigators (Sihler, Cippolone, Peroncito). Only Giacomini (1898) kept to a different opinion. He supposed that only sensory fibres supply the muscle spindle. Leaving aside for the time being the question of the physiological nature of the nerve fibres, related to the muscle spindles, I shall try to describe them in snakes according to my own observations.

Usually, one thick medullated fibre approaches the enlarged part of the muscle spindle. Before reaching this it may divide into two or three branches, all of which in this case enter the muscle spindle. There, where the nerve fibres or its branches enter the spindle, Henle's membrane becomes continuous with the capsule of the spindle and the fibre, or its branches reach the muscle fibre, place themselves parallel to its length and for some distance accompany it, preserving their medullated membrane.

Afterwards they lose the latter and continue as non-medullated nerve fibres to the place of their termination. Along this course they become moniliform, displaying sometimes more or less considerable expansions; sometimes they become ribbon-like and with spiral rings, they embrace the muscle fibre. They give off a considerable number of fine collaterals and together with these they form a bunch of thin ramifications which finally terminate in all probability on the surface of the muscle fibre, without penetrating into its depth. The described relations are so variable in every individual case, especially in the so-called large muscle spindles, that it is difficult to give an exact description.

One circumstance, however, may be stated with positiveness, that these fibres are always medullated and always terminate in the enlarged part of the spindle, inside its capsule. These fibres undoubtedly belong to the cerebro-spinal nervous system and by all authors, with very few exceptions (Bremer), they are accepted for sensory fibres.

However, besides the above described fibres, the muscle spindle is always supplied with a certain number of non-medullated fibres. These fibres terminate in characteristic plates, "*terminaisons en grappes*," which were described in detail above. It is remarkable, that every muscle fibre of a spindle is supplied with several plates (five to seven, perhaps more), as has been established by many investigators (Giacomini, Cipollone). Also all investigators point out that the non-medullated nerve fibres always terminate with



their plates *outside the encapsulated part of the muscle fibre*. In this respect my observations are in contradiction with the generally accepted opinion. As Plate-figs. 10 and 11 show, the medullated nerve fibres on leaving the mixed nerve stem, direct themselves along the muscle spindle in the form of a more or less considerable bunch of fibres. On the way the non-medullated fibres penetrate into the encapsulated part of the muscle spindle and terminate there. I could not establish with positiveness the method of their termination, but I think these terminations do not differ essentially from the terminations lying outside the encapsulated part of the spindle. In other words, I hold that the non-medullated fibres terminate on the surface of the muscle fibre with ramifications of nerve threads, in the shape of plates "en grappes." In my drawing, it can be clearly seen that the non-medullated nerve fibres that approach the muscle spindle, do not all penetrate into the encapsulated part of the spindle. Some of them pass to the non-encapsulated part of muscle fibre outside the spindle (whereas the terminal nerve threads usually divide dichotomously), and always terminate in the same way with the plates "en grappes." Of course, these terminations have no granular lining. The majority of investigators regard these fibres as motor, evidently as a result of the works of Kerschner, Cipollone and Perroncito, who unanimously declared that the non-medullated nerve fibres forming the terminations "en grappes," appear to be only collaterals of the ordinary motor fibres, terminating in motor plates.

I cannot attribute, however, any finality to these observations, without further evidence. So far as my own observations go I have never seen the collateral of a motor fibre giving a termination in the form of a "terminaison en grappe" and it seems to me, that the categorical declaration of Perroncito in this sense (for lizards) has no sound foundation.

Nevertheless, I for my part accept the view that the described non-medullated nerve fibres with their characteristic terminations "en grappes" belong to the motor sphere. I also think it quite possible that these non-medullated fibres are motor fibres belonging to the sympathetic system. Although there are as yet no sufficiently precise data at my disposal to enable me to affirm this with positiveness, I have some evidence which I hope to set forth on a future occasion. So far I can only express my opinion in the form of a supposition.

I conclude this article with the description of nerve cells which I have observed along the course of the peripheral nerves in the muscles of the abdominal wall in Python. They are found here in the shape of more or less considerable accumulations (ganglia) or spread about in groups of two or three cells or even singly. They are all, however, of one type—the so-called unipolar cells. In the cells of this type, one thick process leaves the body of the cell, and after a short course divides into two branches—one running centrally, the other peripherally. These cells are bound up with the small nerve stems, usually of a mixed composition of medullated and non-medullated fibres.

It is difficult to say with positiveness whether medullated or non-medullated

fibres are connected with these ganglion cells. I think, however, that they are connected with non-medullated fibres since in one of my preparations I succeeded in finding a nerve cell of this unipolar character actually in the nerve termination itself—in the end plate of the “second type” (fig. 12). All investigators are agreed that the non-medullated nerve fibres terminate in the plates of the “second type,” and therefore in this case it is necessary to accept the conclusion that the nerve cells in question are connected with the non-medullated nerve fibres.

Besides, I have never observed any ganglion cells along the nerve bundles formed only of medullated fibres. I think it necessary to remark that nerve cells, in the form of more or less considerable ganglia or isolated, are found in the peripheral nervous system in very many places, in the plexuses of the intestinal canal, in the tongue, the salivary glands, pancreas, uterus, etc.,

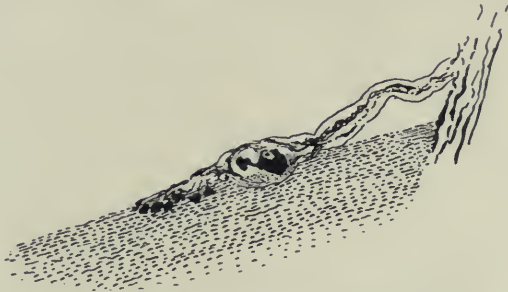


Fig. 12. Nerve cell situated in nerve termination (type II). Python.

but in the nerves of muscles they have very seldom been described. I think they were accurately described for the first time in the *m. lingualis* of the frog by Bremer (1883).

#### SUMMARY

1. In the muscles of snakes there are two forms of nerve terminations—of the 1st and 2nd type. Both kinds belong to motor nerve fibres. The difference between them, however, is so great, that involuntarily one is forced to think of the double innervation of these muscles from the side of the cerebrospinal nervous system (medullated fibres) and the sympathetic system (non-medullated fibres).

2. In the muscles of snakes, nerve bundles of mixed character are found and they are composed of three kinds of fibres: (*a*) medullated nerve fibres, terminating in muscle fibres, in the usual motor end plates (type I), (*b*) non-medullated nerve fibres, also terminating in motor plates in muscle fibres (type II), and (*c*) non-medullated nerve fibres terminating in the intramuscular connective tissue with free terminations.

3. The position of the motor end plates (type I) is quite definite; they lie under the sarcolemma (hypolemmally). The position of the plates of type II is as yet doubtful. There is reason to believe that they lie on the surface of the muscle fibre not under the sarcolemma, but outside it (epilemmally).

4. Muscle spindles in the muscle of snakes are of two kinds, small (fuseau à terminaison circonscrite) and large (fuseau à terminaison étendue, according to French authors). They represent the sensory organs of muscles in snakes. They are also always supplied by medullated fibres as well as by non-medullated.

The medullated fibres always enter the encapsulated part of the muscle spindle, and the fibre preserves its medullated sheath, independently of whether it enters singly (small spindles) or by ramifications (large spindles). The nerve fibres of this kind are sensory.

At some distance from the place of their termination, they lose their medullated sheath and terminate with their terminal ramifications on the surface of the muscle fibre, which they sometimes accompany a considerable distance, but always within the limits of the encapsulated spindle.

The non-medullated nerve fibres enter the encapsulated part of the spindle in thin bundles, as a rule separately from the medullated fibres. They also terminate on the surface of the muscle fibre of the spindle and I hold that these terminations are similar to those on the non-encapsulated part of the fibre, these latter appearing as typical plates of the 2nd type.

These non-medullated fibres are motor. It is probable that they do not belong to the cerebro-spinal nervous system but to the sympathetic.

5. I have not observed in the muscle of snakes the ultraterminal fibres of Ruffini and Perroncito. As to the collaterals, described by Perroncito, their existence is undoubted. However, according to my observations, they enter together with their principal fibre into the same muscle fibre and can participate in the formation of an ordinary terminal plate, or in other cases, can terminate in an independent, so called, additional plate with the same structure as the main plate.

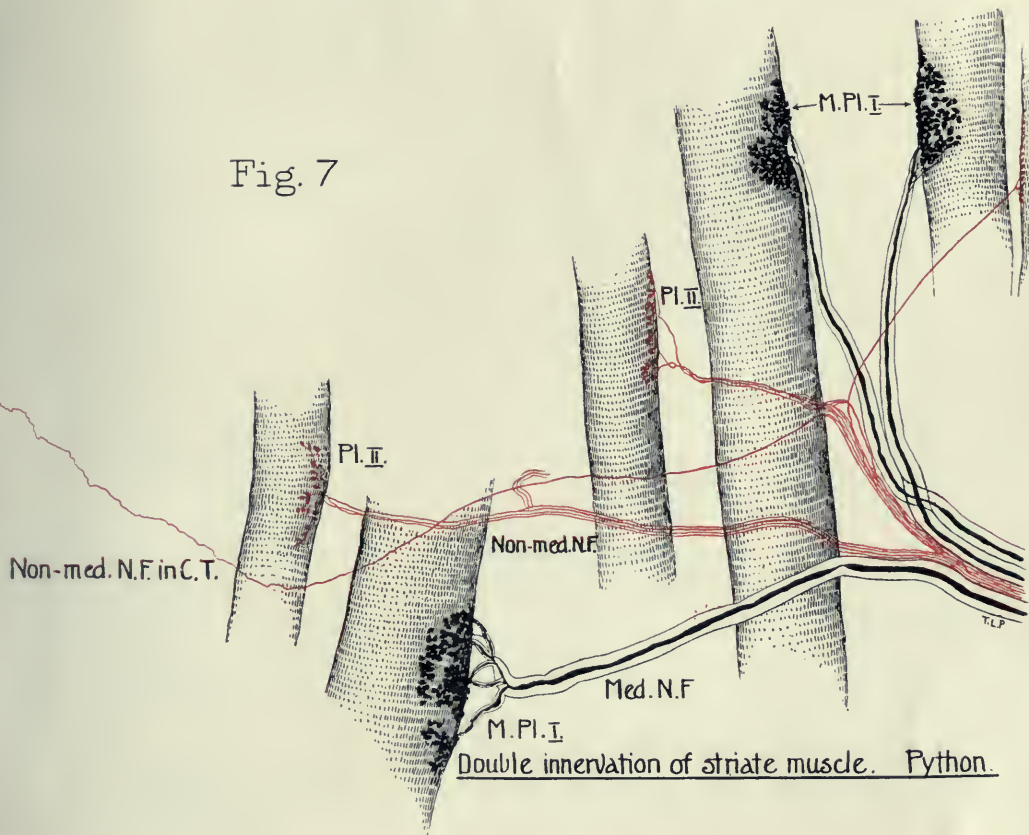
6. In the course of the nerves supplying the abdominal muscles, groups of nerve cells are observed, which form sometimes more or less considerable ganglia, or they may be found singly along the whole extent of the nerve bundle, in rare cases even in immediate proximity to the nerve termination. These cells are unipolar and the single process leaving the body of the cell divides after a very short course into two branches, central and peripheral. Both branches seem to be non-medullated.

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Fig. 7





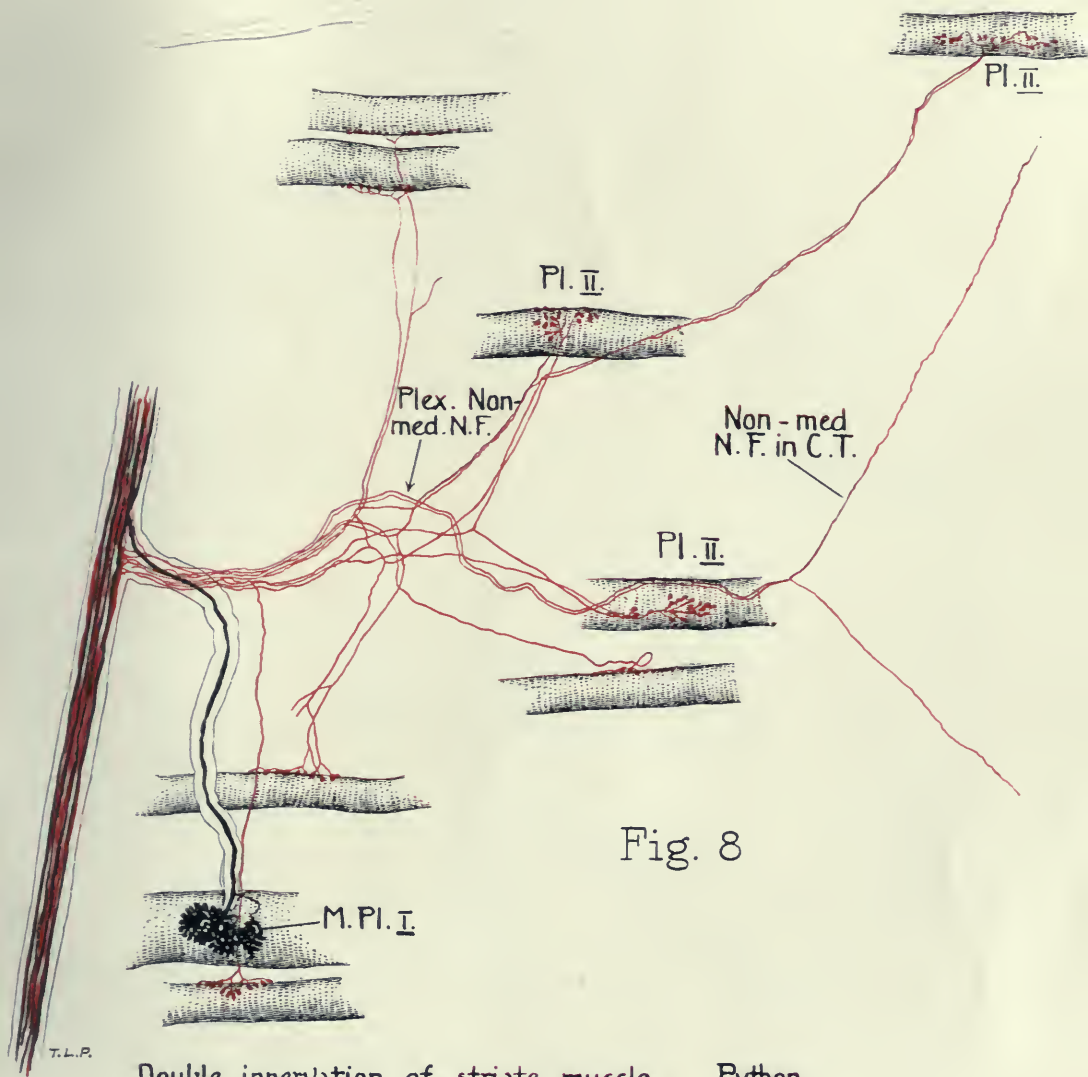


Fig. 8

Double innervation of striate muscle. Python.





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Fig. 10

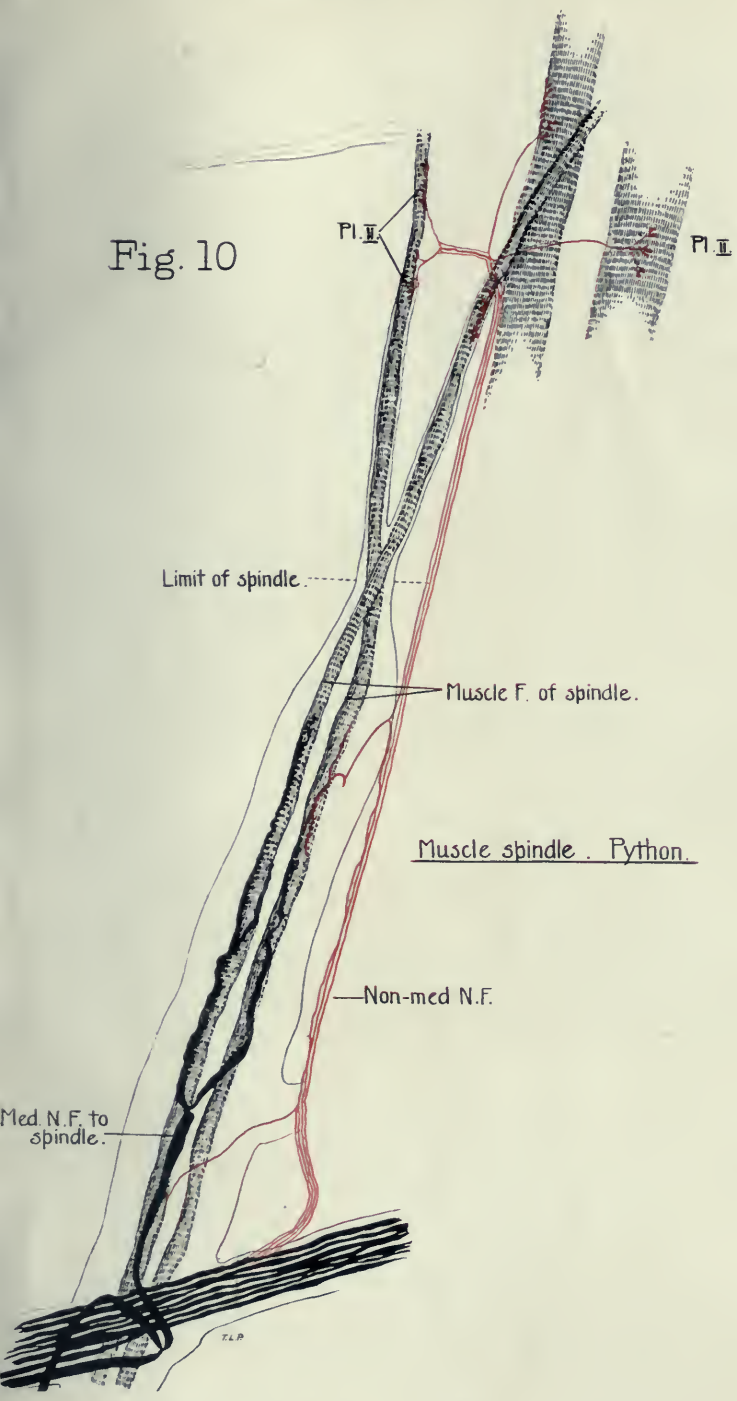


Fig. 11







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## A NOTE ON THE POST-NATAL GROWTH OF THE KIDNEY, THYROID GLAND AND LIVER

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At a previous meeting of the Anatomical Society in 1915, I showed a specimen of "Single Kidney," which as a result of congenital absence of the opposite kidney, had undergone a compensatory enlargement to approximately double the size and weight of the normal organ. I was much impressed at the time by the circumstance that this enlargement was due to an increase in the size of the constituent parts or units rather than to an increase in their number. Thus the size of the pyramids in the hypertrophied kidney was double that of the pyramids in the normal kidney; while their number corresponded to the average number found in the normal kidney although the latter is only half the size of the "single" kidney. Further on microscopical examination the Malpighian corpuscles and tubules of the hypertrophied kidney were seen to be much larger than those of the normal control kidneys (fig. 1). Moreover the total number of glomeruli in the enlarged single kidney was found to be approximately the same as that present in the normal kidney. This was estimated by counting the number of glomeruli which were included in 16 squares of equal size, ruled on a glass disc, fitted into the eye piece of the microscope; taking the average of a series of such counts, and comparing this with the average of an equal number of observations in normal control kidneys. It was found that the number of corpuscles in a given number of squares in the single kidney was approximately half that in an equal number of squares in a normal kidney. In other words in any given field of the microscope, the number of glomeruli seen in a typical part of the cortex of the hypertrophied kidney was approximately half that of a corresponding part of the cortex of a normal adult kidney. It may be assumed therefore that since the hypertrophied single kidney is double the size of the normal kidney, the total number of Malpighian corpuscles in it will approximately correspond with the total number in the normal kidney, and that the enlargement is a true hypertrophy, rather than a hyperplasia.

Now if sections of a normal adult kidney are compared with sections of the foetal kidney at birth, a striking difference is seen in the size of the glomeruli and tubules and of the number of glomeruli which appear in the field of the microscope. The glomeruli and tubules of the foetal kidney are much smaller and in any given field of the microscope they are very much more numerous. The proportion as estimated by counting the number in a series of squares,



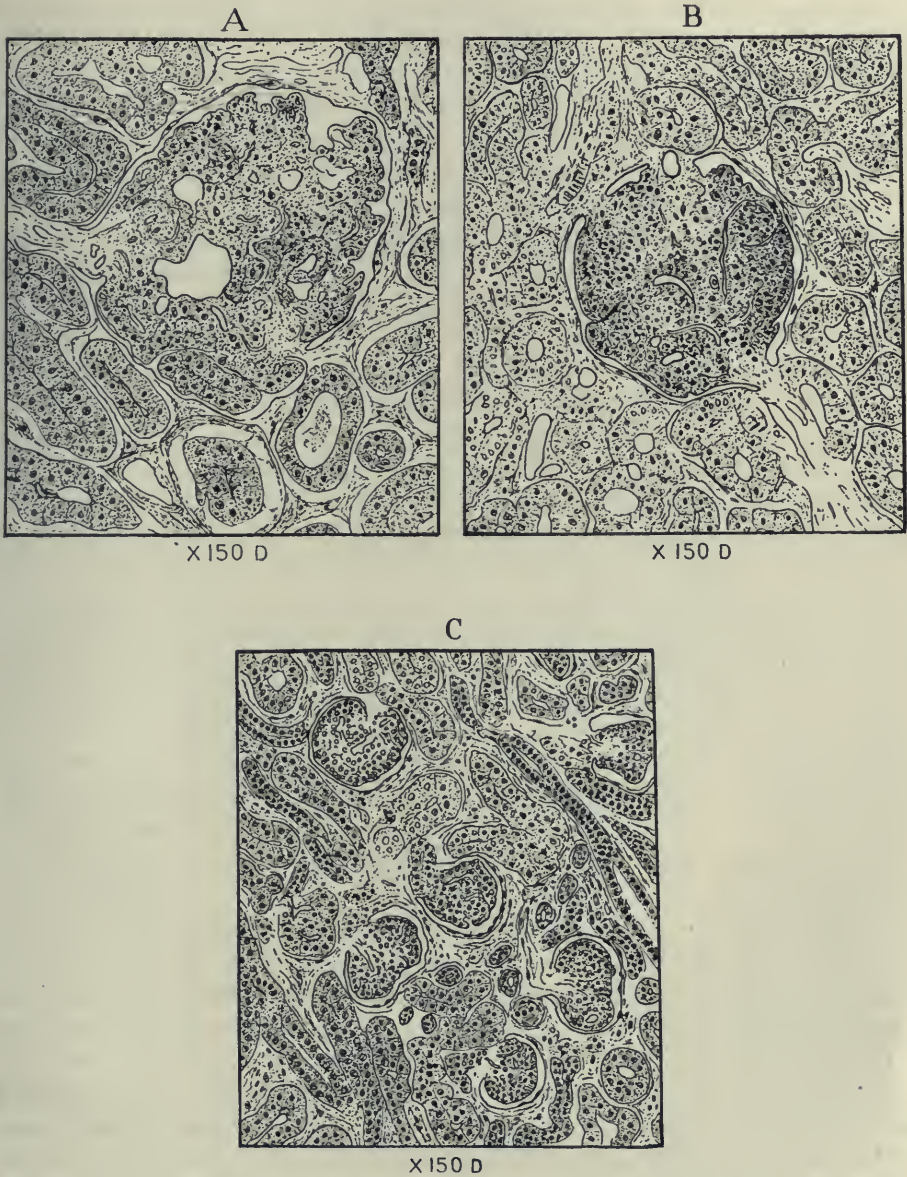


Fig. 1. Camera lucida drawings of sections of *A*, an hypertrophied "single kidney," *B*, a normal adult kidney, *C*, a foetal kidney at birth. The drawings were made at the same magnification (150 diameters) and show the large size of the glomerulus and tubules of the single kidney as compared with the adult normal kidney; and the large number of small glomeruli and tubules appearing in the field in the foetal kidney as compared with the adult organ.



I found to be 100 in the foetal kidney to 6.6 in the adult organ; or expressed in a different way: in a given area of the whole width of the cortex of the foetal kidney, there would be approximately 15 times as many glomeruli as in a corresponding area of the adult organ viewed under the same magnification.

Now the average weight of the normal adult kidney, as stated by H. Vierordt, *Daten u. Tabellen für Mediziner*, is 152 grammes, and of the new-born child 10.5 grammes; or, in other words, the adult kidney is approximately 14.4 times the weight of the kidney at birth. The figures suggest that the number of glomeruli present in the kidney of a new-born child is approximately the same as in the adult. The glomeruli of the foetal kidney, however, vary



Fig. 2. Camera lucida drawing showing the relative size of the muscle fibres and their nuclei in the uterus of *A*, a child aged 6½ years, and *B*, the uterus of a woman at the end of pregnancy. The magnification in each case was 850 diameters.

considerably in size and appearance in different zones, thus they are small and flattened near the surface, larger and more spherical in the deeper parts of the cortex. The peripheral glomeruli are obviously in process of formation and are incompletely developed. According to Kültz it is not until the close of the second year that the peripheral glomeruli have reached the size of the central, when the average size of the peripheral glomeruli is  $157\mu$  and of the central  $158\mu$ . They afterwards increase equally in size, and nearly attain their full diameter at puberty.

The question of whether the enlargement of a single kidney associated with congenital absence of the other kidney is due to proliferation of the units

(hyperplasia) or enlargement (hypertrophy) has been investigated by Boycott, Galeotti and Santa, Eckardt and F. C. Moore.

In Boycott's case which occurred in a rabbit, he found by direct enumeration of the glomeruli, in serial sections cut from a block of the single kidney, and corresponding in weight to similar blocks cut from two normal control kidneys, that the enlarged single kidney would according to this means of estimation, have had only the same number of glomeruli as were contained in a normal kidney half its size. Thus the enlargement of the single kidney in his case, as in mine, was an example of hypertrophy and not hyperplasia. The glomeruli and tubules were also carefully measured by Boycott and found to be considerably larger than in the normal; the average diameter of the glomeruli of the single kidney in the rabbit, being  $40\mu$  and of the controls  $33.8\mu$ . The relative volumes being, of the single kidney 33, of the controls 19; the increase in volume of the glomeruli in the single kidney thus being 1.7 times that of the controls. Somewhat divergent results were obtained by Galeotti and Santa working with rabbits in which a unilateral nephrectomy had been performed; and by Eckardt and Moore who recorded observations on congenital cases. These have been reviewed and criticised by Boycott in the article alluded to above. In a case of multiple anomalies occurring in a foetus described by H. A. Harris, in which there was agenesis of one kidney, the remaining kidney was found by him to be normal in size and position. This case will be alluded to later, in discussing the influence of function in producing hypertrophy of organs.

Several factors appear to be concerned in producing the divergent results which have been obtained by different observers, as regards the size and number of the glomeruli in an enlarged single kidney, and in the normal adult kidney respectively.

The diameters of the glomeruli as seen in sections, obviously vary considerably according to the plane at which the glomerulus is cut. Moreover, as the glomeruli are often flattened it is necessary to take the mean of two principal diameters at right angles to each other. Further in the foetal kidney and in the infant, as has been stated above, the glomeruli near the surface of the cortex are flatter and smaller than those nearer the medulla. Moreover, apart from pathological changes occurring as the result of a condition such as chronic interstitial nephritis, there appears to be a considerable range of variation in the normal kidney as regards the size of the glomeruli and the amount of space occupied by the tubules and the supporting connective tissue between the glomeruli. The estimated average diameter of the glomeruli in the adult kidney as computed by different authors varies from  $167\mu$  to  $237\mu$ . This difference may be explained in part by different methods of fixation of the tissues, some fixatives causing a greater degree of contraction than others, e.g. strong solutions of formalin, alcohol or the mineral acids, but it is probable that there is also a considerable range of variation in the normal kidney. Apart from these considerations the diversity of results which have been obtained



by different authors with regard to enlargement of a single kidney being due to hypertrophy, or to hyperplasia, or to both these factors, may be due in part to the fact that a single kidney is often affected by nephritis, which if of long standing, and of the chronic interstitial type, may result in a considerable shrinkage of the supporting connective tissue, bringing the glomeruli and tubules nearer together and by compression diminishing their size. Further, a small increase in the diameter of spherical structures means a large increase

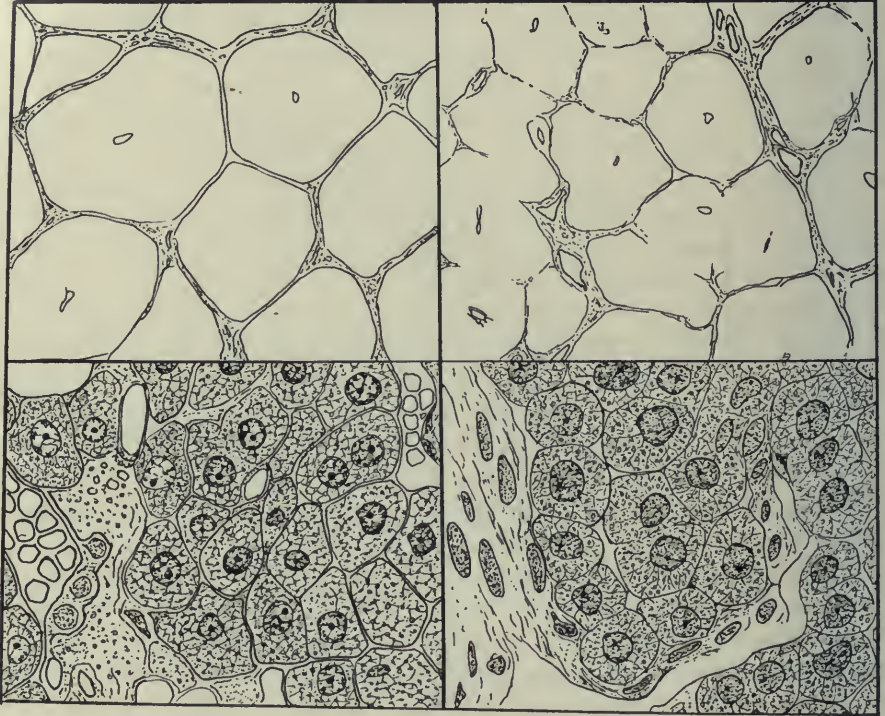


Fig. 3. Camera lucida drawings showing the relative size of the lobules, and cells of the adult human liver, as compared with the foetus at birth. The upper sections of the figure represent the lobules in outline as seen under a low power, the constituent cells not having been represented. The lower sections show the hepatic cells under a high power of magnification. The drawings on the left side of the figure are of a normal adult organ, and on the right side of a foetal kidney at birth.

in their volume, and if the diameter of the glomeruli only is observed, the volumetric increase is perhaps not fully appreciated.

The important part which enlargement of the units, viz. secreting cells, tubules, glomeruli and pyramids, takes in the growth of the kidney, led me to enquire whether this enlargement takes place to any extent in the growth of other organs of the body. We are all familiar with the enormous increase in size which takes place in the growth of the ova and in the ganglion cells of the central nervous system, and of the posterior root ganglia; and a consider-



able part of the enlargement of the ovary, and the ganglia on the posterior roots of the spinal nerves must be due to this cause.

In discussing the growth of striated muscle fibres Schäfer states that "the muscular fibres, after having acquired their characteristic form and structure continue to increase in size until the time of birth, and thenceforward up to adult age. In a full grown foetus most of them measure twice and some of them three or four times their size at the middle of foetal life, and in the adult they are about five times as large as at birth.

Further the enlargement of the uterus during pregnancy is a familiar instance of an increase in bulk of a tissue accompanied by increase in the size of the constituent elements. Selheim represents the increase in length of the plain muscle fibres of the pregnant uterus at term as being approximately seven times that of the cell-body of the muscle fibre in the non-pregnant condition, and the length of the nucleus as approximately four times that of the non-pregnant condition. In fig. 2, *A* represents the muscular wall of the uterus, from a child 6½ years old, and *B* that of a pregnant uterus at the end of term, the nuclei of the latter are 4.3 times the length of the muscle nuclei in the child. This may be regarded as a physiological hypertrophy and is very similar to the hypertrophy of a muscle due to increased use of the muscle, and the pathological hypertrophy of muscle in cardiac obstruction, or hypertrophy of the urinary bladder due to stricture of the urethra, or enlargement of the prostate. It is probable that all are accompanied by increased vascular supply and nutrition. The enlargement of the cock's spur in Hunter's experiment of grafting the spur into the comb, is another example of hypertrophy due to increased vascular supply.

The hypertrophy of muscle resulting from increased strain or use, suggests that the enlargement of a gland may be correlated with an increase of function. The kidney, with the increased function of the organ which takes place at birth and of the mammary gland, preparatory to lactation may be cited as examples. I therefore examined other glands such as the liver and thyroid to ascertain what changes could be observed in the unit structures in the adult as compared with the same structures at birth. In the normal human liver, fig. 3, drawn from a specimen kindly prepared for me by Dr da Fano, it will be observed that there is a slight increase in the size of the lobules in the adult as compared with the foetal, but it is difficult to obtain exact measurements owing to the incomplete demarcation of the lobules in the human foetal liver. On examining the hepatic cells, the adult cells are seen to be more elongated, more flattened by compression, and to have a more coarsely granular cytoplasm, than the foetal, but their size is approximately the same as in the foetus, and the nuclei considerably smaller, their average diameter being about  $6\mu$  as compared with  $8\mu$ , the average diameter of the nucleus of the foetal hepatic cells. The cell-bodies of the latter are more rounded and their cytoplasm more finely granular than the adult. It is obvious that in the growth of the liver there must be a great increase in the number of the lobules and of the hepatic cells.

In the post-natal growth of the thyroid gland (fig. 4) there is a marked increase in the size of the follicles, accompanied by proliferation of the epithelial cells lining their walls, and in the formation of colloid. The secretory cells as in the liver are more elongated than in the foetus, and their nuclei smaller. They vary considerably in size, whereas the rounded foetal cells are much more uniform in size. The number of cells lining the adult follicles is much greater than that in the foetus; growth must therefore be accompanied by a considerable amount of proliferation of the secretory cells.

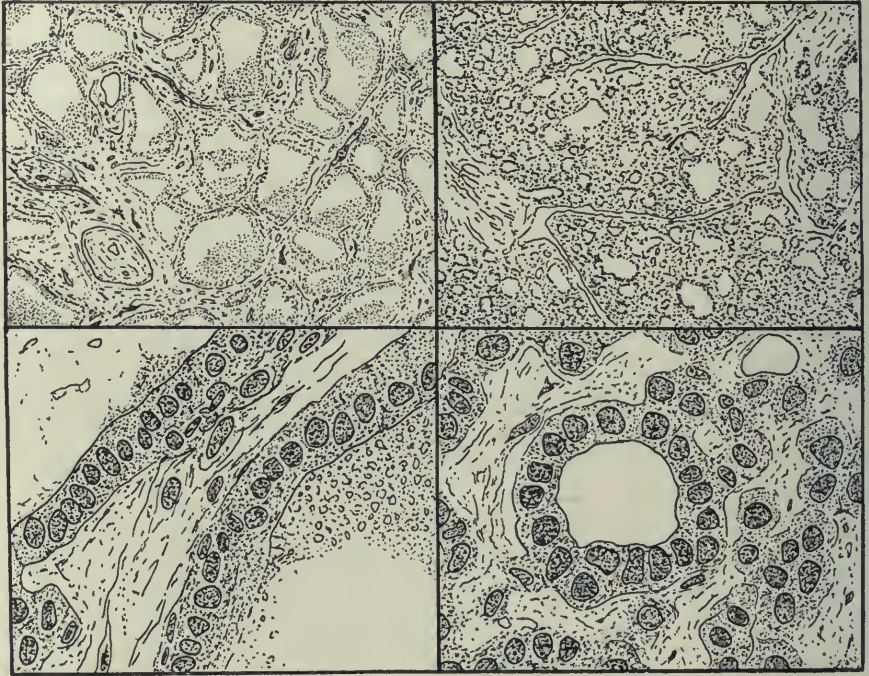


Fig. 4. Camera lucida drawings of the normal adult and foetal thyroid gland. The upper sections, drawn under a low power magnification, show the large size of the vesicles in the adult organ, as compared with those of the infant at birth. The lower sections, drawn under a higher power of magnification, show the relative size and shape of the individual cells lining the follicles. The drawings of the adult organ are on the left side of the figure, those of the foetus at birth on the right.

Other organs such as the supra renal bodies and thymus gland have been examined, but as in the normal life history of these glands the replacement of the original cells is very great, any observations on the relative size of the constituent parts is of little value from the standpoint of this enquiry.

In summarising the growth changes which take place in the kidney, it is obvious that a large part of this growth is due to enlargement of the unit structures such as the tubules, glomeruli, and pyramids, and that the enlarge-

ment of the single kidney in cases of absence of the other is largely due to a true compensatory hypertrophy.

An interesting case was recently reported by Mr H. A. Harris, in which a single kidney was found in a foetus presenting a combination of rare anomalies. He states that the single kidney was normal in size. If the marked enlargement of the glomeruli and tubules which takes place in infancy is associated with the increase in function which takes place after birth, this absence of compensatory enlargement of the organ in a foetus prematurely born at the 27th week, is readily explained on the assumption that the full physiological action of the kidney had not yet been developed.

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## CASE OF ABNORMAL DUODENUM

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THE abnormality here recorded was observed in the dissecting room, Oxford University in January, 1923, in a man aged about 56 years, who had died of no trouble in connection with his alimentary tract. The condition is reported as being of some interest from the developmental point of view, and also because of its rarity.

### DESCRIPTION

*1st part.* Normal.

*2nd part.* Vertical in position and containing openings of bile duct and pancreatic duct separate but situated about the normal level.

The relations and arrangements are normal except for its posterior relation. At its lower extremity it turns abruptly and directly backwards and passed into

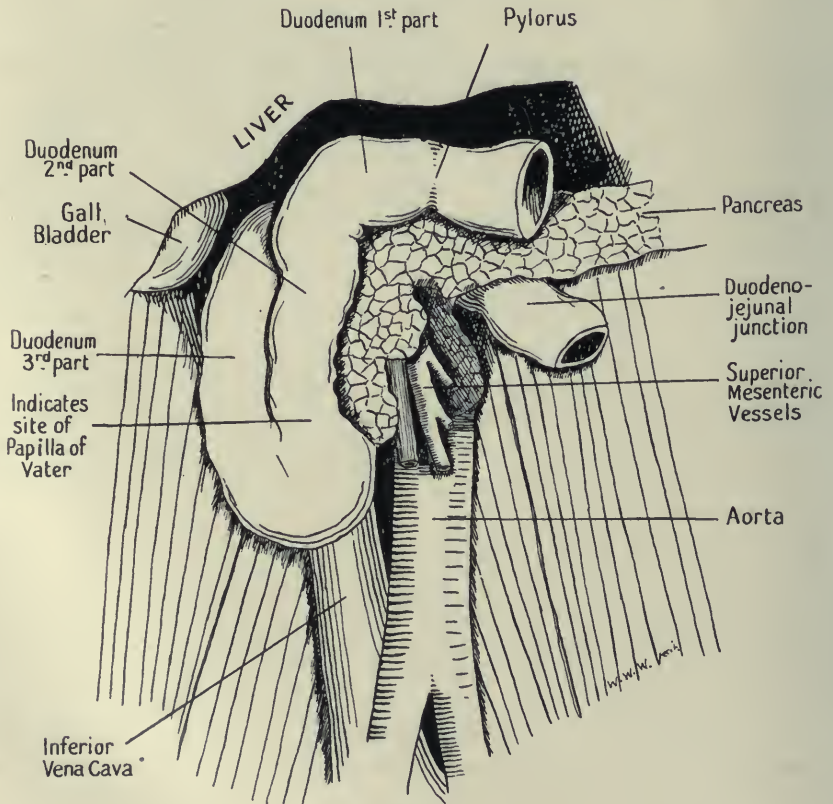


Fig. 1

## 3rd part.

(a) Vertical limb runs up parallel with and behind 2nd part and is approximately of the same length. It is in close relation with the liver and neck of gall-bladder. After a course of approximately 3 ins. it turns sharply to the left passing into

(b) Transverse portion (*vide* diagram). This runs transversely and somewhat downwards to reach the duodeno-jejunal junction which is situated in about the normal position on the left side of the body of the 2nd lumbar vertebra.

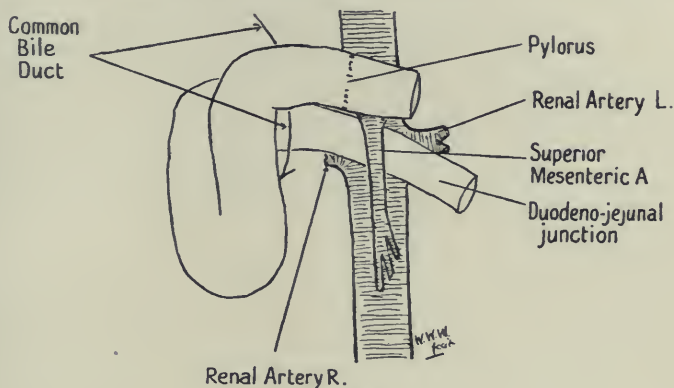


Fig. 2

In its course this part of the duodenum passes behind the neck of the pancreas and under the superior mesenteric vein and artery. The common bile duct also lies in front of this portion. It lies directly in front of the left renal vein crossing that vessel and the aorta.

Between the upper end of the 2nd part on its right and posterior aspect and the upper end of the vertical limb of the 3rd part on its right and anterior aspect there stretches a firm band approximately  $\frac{1}{2}$  in. long,  $\frac{1}{4}$  in. wide, and  $\frac{1}{16}$  in. thick.

## REMARKS

The condition is a developmental one and is apparently due to rotation of the duodenum loop through a complete half-circle in the clockwise direction. The cause of this is not obvious and it is a question what part if any the band of adhesions noted between the 2nd part and the vertical loop of the 3rd part has played in the production of this condition. Possibly the band is a purely secondary condition.

The condition has been described by S. V. Telfer<sup>(1)</sup> and by J. H. Anderson<sup>(2)</sup>. I can find no other reference to the condition.

I am indebted to Professor Thomson for permission to publish this note and for his whole-hearted assistance especially in the preparation of the figures.

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## REVIEW

*X-Rays:—Their Origin, Dosage and Practical Application.* By W. E. SCHALL, B.Sc. (Lond.), F.Inst.P. (John Wright & Sons, Ltd., Bristol.) 5s.

This book is the successor to *Electro Medical Instruments and their Management*, which was published in 1892. Like its predecessor it serves a double purpose. It provides the student of Radiology with a lucid elementary textbook, and the well-known firm of Schall and Son, London, with an excellent advertisement. As such it is issued free to medical practitioners and others interested in X-ray work.

The first section deals with the origin of X-rays and their properties, electrical apparatus, X-ray tubes, and the measurement of X-rays, with special reference to dosage for therapeutic purposes. It contains much useful information, especially that part dealing with electrical apparatus.

In the second section, which deals with the practical application of X-rays for diagnostic and therapeutic purposes, the author presents a concise account of modern methods gleaned from the writings of many radiologists and physicists.

One feels in reading this section that the author, by lack of medical experience is treading on dangerous ground and that he feels so himself is evident by his explicitly disclaiming "all legal responsibility" in connection with tables for dosage "if it should be found that any error is contained in them."

It is a book which, within its limitations, will be of use to medical students and radiologists.

J. M. W. M.



# THE ANTERIOR END OF THE NEURAL TUBE AND THE ANTERIOR END OF THE BODY

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“Remove not the ancient landmark which thy fathers have set.” *Proverbs* xxii. 28.

IN July 1922 I advanced certain criteria which I considered to be of the utmost importance in the classification of musculature. It was necessary in order to

## JOURNAL OF ANATOMY

THE expenses of illustrating Dr Kulchitsky's paper on “Nerve Endings in Muscles,” published in the January number, and of Drs Colwell, Thompson and Wakeley's paper on “The Effects of X-Rays upon the Skin of the Frog Tadpole,” have been defrayed by the Medical Research Council.

The Editors of *The Journal of Anatomy* take this opportunity of acknowledging their indebtedness to the Medical Research Council.

mesoderm and then to show what light this embryonic history throws upon the two questions raised in the title of this paper.

## THE ORIGIN OF THE SEGMENTED MESODERM.

In 1894 Lwoff put forward two conceptions concerning the origin of the segmented mesoderm at that time regarded as extremely unorthodox, which are given in his own words in the following statement:

Das Hauptergebniss dieser Untersuchung ist, dass die Einstülpung bei *Amphioxus* keineswegs als einfache Gastrulation zu betrachten ist, als es bisher angenommen. Es sind vielmehr hier zwei verschiedene Processe zu unterscheiden: erstens die Einstülpung der Entodermzellen, aus denen der

Darm entsteht; zweitens die Einstülpung der Ektodermzellen vom dorsalen Umschlagsrande aus, welche die ektoblastogene Anlage der Chorda und des Mesoderms bildet. Die Einstülpung der Entodermzellen ist als Gastrulation zu betrachten. Es ist ein palingenetischer Process, den die Chordaten von ihren Vorfahren ererbt zu haben scheinen, wo dieser Process gleichmässig und radial symmetrisch vor sich ging, wie es sich bei einigen wirbellosen Thieren beobachten lässt. Die Einstülpung der Ektodermzellen ist dagegen als ein caenogenetischer Process zu betrachten, der mit der Bildung des Darmes nicht zu thun hat und durch den die Bildung der ektoblastogene Anlage der Chorda und des Mesoderms eingeleitet wird.

It will be readily appreciated that the two significant conceptions introduced here by Lwoff are (a) the postulate of a caenogenetic *second phase* in chordate development; the tissue of which gives rise to the chorda dorsalis and the segmented mesoderm and (b) the postulate that this *second phase* which provides the tissue giving rise to the chorda dorsalis and the segmented mesoderm is an *invagination of ectoderm cells*.

Nobody need be reminded of the fact that the first phase (the palingenetic phase or gastrulation proper), to quote Brachet (1921, p. 117), is "le processus grâce auquel, aux dépens de la masse des cellules issues de la segmentation de l'œuf, se constitue une larve à deux feuillets, l'un externe, l'autre interne, qui restent en continuité entre eux en un point déterminé de leur étendue. La gastrula est donc, dans tous les cas, un embryon didermique." This phase has for its objective the laying-down of the gut and its derivatives and the formation of that ancestral gastrula type postulated by all embryologists since the appearance of the classical research of Huxley (1859) when he established the homologies of the ectoderm and endoderm of Coelenterata with the same layers in Vertebrata. It is the same ancestral type whether we regard its endoderm as being produced by invagination (as in Haeckel's *gastraea*, 1872), by delamination (as in Lankester's *planula*, 1877), by transverse fission (as in Bütschli's *plakula*, 1884), or by immigration (as in Metschnikoff's *parenchymella*, 1886)—*vide* McMurrich (1890). The term *didermique* used by Brachet is therefore singularly apt in summarising the end result of this first phase.

We may therefore assume that all investigators are unanimous in recognising a *didermic* or first phase of "gastrulation," whatever the differences of opinion may be concerning the actual *method* of achievement of the phase.

As regards the second phase, it is perfectly true that even before the time of Lwoff various observers had recognised that the process of invagination in Chordata was not a single but a double one. However, Lwoff appears to have been the first to realise that the second phase had one objective only and that this objective was the formation of the tissues of directive movement, i.e. the segmented mesoderm and the notochord. He therefore was the first to really define it and certainly did a great service by conceiving it as a unified and separate process superimposed upon the first phase. Since the time of Lwoff, this second phase has been repeatedly recognised—by Brauer (1897), Brachet (1902), O. Hertwig (1903), Hubrecht (1905), Keibel (1905), and Selys Long-

champs (1910)—and has become practically part and parcel of present day embryological orthodoxy.

The actual nature of the events which lead to the production of the second phase of gastrulation will be apparent immediately if fig. 1 (representing diagrammatically the invagination process in an Amphibian form) be examined. This diagram (after Brauer) shows the blastoporal opening posteriorly. The ventral (or posterior) boundary of the blastopore is formed by large rounded and richly yolk-laden cells which present the strongest possible morphological contrast to these endodermal cells as regards their size, shape and cellular content. They are deficient in yolk and are richly supplied with pigment so approximate much more closely in character to the ectoderm. These cells may be traced forward as a continuous plate lying under the ectoderm. This plate terminates suddenly and is supplanted anteriorly by two endodermal cells (i.e. at the point of transition). This "dorsal plate" (or deutenteric arch of Brachet) gives rise to the notochord and the segmented mesoderm. We see in it therefore the accomplishment of the second phase in gastrulation.

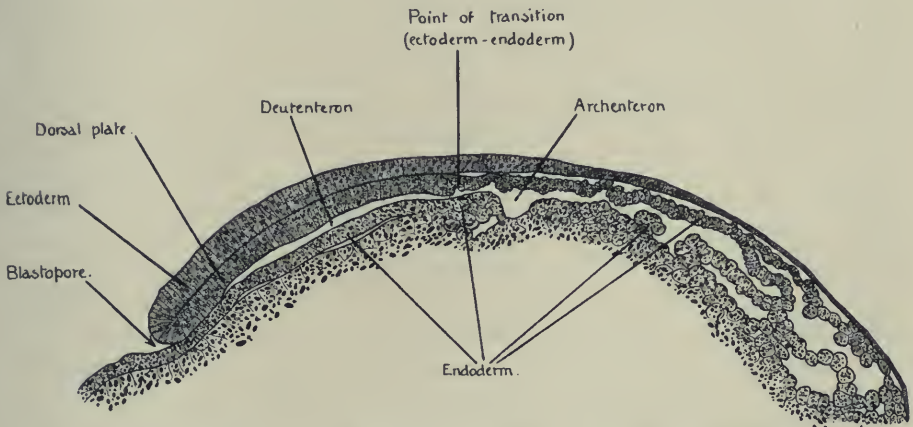


Fig. 1 (after Brauer) to show the two phases of vertebrate gastrulation.

So obtrusive are these two phases in *Petromyzon* that Selys Longchamps (1910) ultimately named the cavity lying under the primordium of the chorda and the segmented mesoderm the *deutenteron*, as opposed to the *archenteron* which is present more anteriorly in the embryo and arises before the *deutenteron*.

The "enteric" cavity covered over by this dorsal plate of mesodermal tissue in the amphibian (*vide* fig. 1) is the *deutenteron* (of Selys Longchamps); anterior to it we recognise the *archenteron* which becomes formed gradually and lined by true endoderm cells.

This conception of the second phase has found admirable treatment in Brachet's (1921) work, where it has been demonstrated for *all* the vertebrate



classes. Consequently, there is little need here for a revision of the detailed evidence.

On en a déduit (says Brachet, p. 131) cette conclusion, d'une importance capitale pour la morphologie des Chordes, que l'écusson médullaire et les organes qui lui sont sous-jacents, par conséquent le dos entier de l'embryon, au cerveau antérieur à l'anus, se forment dans la domaine exclusif du deutenteron, par différenciation sur place de l'ectoblaste et de l'entoblaste qui en constituent la paroi superficielle. Nous donnerons à cette paroi le nom de *voûte deutenterique*.

Scarcely has the first phase been completed in lower Chordata (Amphioxus and Petromyzon) when the second phase begins. Indeed, the higher the animal, the greater is the tendency for the second phase to be initiated early and to be expedited so that in the mammalia the second phase is ushered in so rapidly that it may be described as anteceding the first phase. In this precocity in appearance of the second phase we recognise another example of the tendency frequently evidenced in embryonic forms to reproduce, as early as possible in foetal life, the tissues which are more early called into activity irrespective of the order of their appearance in phylogeny. This is of interest because certain authors (*vide* Lwoff's paper) have been misled by this precocity into regarding the second phase as *palingenetic* instead of *caenogenetic*, a deduction which other considerations will not allow us to admit.

It is evident, therefore, that the first postulate of Lwoff—the unified and separate process superimposed upon the first phase—is well grounded in embryological fact. Further, since this process gives rise to the segmented tissues it is evident that the *second phase* and the *deutenteron* are peculiar to the possessors of a segmented mesoderm.

The second postulate of Lwoff—the *ectodermal* origin of the notochord and segmented mesoderm—has not been generally admitted by embryologists. Selys Longchamps and Brachet, amongst the recent Continental workers, still regard these tissues which arise from their “deutenteric arch” as *endodermal* in origin—a view dating from Kowalevsky's and Hatschek's classical researches upon Amphioxus and maintained by Conklin (1905) for the Ascidian.

An insistence upon the *endodermal* origin of these tissues has been rendered very easy by its general adoption in most embryological text-books since Hatschek's time. Nor is the reason for this insistence far to seek. The cogent impulse behind the attempt to derive the segmented mesoderm from the endoderm is the establishment of an homology between the “outpouchings of the archenteron” in Echinodermata and the so-called “outpouchings of the archenteron” in Chordata; i.e. the demonstration of an homologous process of mesoderm-formation in both phyla.

There are two reasons why such a doctrine is untenable. In the first place, the two tissues called “mesoderm” produced by these supposedly homologous processes are in no way comparable with one another. Thus the “outpouchings

of the archenteron" in Echinodermata give rise to a water-vascular system and other structures peculiar to Echinodermata; in brief, the resultant "mesoderm" is unsegmented and is innervated by a characteristic nerve-net system. The embryological investigation of Echinoderms has tended to emphasise this *endodermal* origin of the unsegmented mesoderm in these creatures; there is present in them, however, an equally important, even if not so obvious, *ectodermal* constituent of this unsegmented mesoderm also innervated by the nerve-net system. The whole "mesoderm" so constituted of endodermal and ectodermal elements and innervated by the nerve-net system may be broadly compared only with the *peripheral mesoderm* of Rückert (the *peristomial mesoderm* of Rabl) in Chordata. In Chordata, this "mesoderm" is equally unsegmented and innervated by the sympathetic system—the nerve-net of these forms.

But the unsegmented mesoderm, common to all Metazoa, is a very different type of tissue from that mesoderm which results from the so-called "outpouchings of the archenteron" in Chordata. This mesoderm is the true or *segmented* mesoderm—the *axial mesoderm* of Rückert (the *gastral mesoderm* of Rabl). There is no tissue of Echinodermata comparable with this segmented mesoblast which is not only innervated by the sympathetic nerve-net system (Boeke, 1913; J. T. Wilson, 1921) but has an additional and characteristic innervation presenting the synaptic neurones of Waldeyer with their specific reflexes and invariability of response—phenomena entirely without counterpart in Echinodermata (Dart, *loc. cit.*).

The second reason why the echinoderm homology is untenable has been adequately dealt with by Lwoff whose statement will be used here. Lwoff has shown that, even though "outpouchings" occur in Chordata, the cavities of the outpouchings do *not* form the coelom as has been assumed in the past; but these cavities *always* disappear and the coelom appears *separately* and *elsewhere*. This repudiation is so important and has been so generally neglected that it should be quoted in full. He says:

Daraus ist klar, dass die Mesodermfalten mit ihren Höhlen bei Amphioxus nur ein äussere zufällige Erscheinung darstellen, der man keine besondere phylogenetische Bedeutung zumuthen kann. Die Leibeshöhle hat hier mit den vermeintlichen Urdarmdivertikeln nichts zu thun. Es ist also nur eine scheinbare Enterocoelie, die in Wirklichkeit nicht existiert, da die Leibeshöhle, wie bei allen Wirbelthieren, *durch Auseinanderweichen der Zellen* gebildet wird. Es darf darum keine Rede davon sein, das Amphioxus streng genommen ein Enterocoelie ist, geschweige denn davon, dass alle Wirbelthiere, was die Mesoderm—und Leibeshöhlenbildung betrifft, von einem Enterocoelie abzuleiten sind. Denn alle Versuche, bei niederen oder höheren Wirbelthieren die Urdarmdivertikel resp. Mesodermfalten und einige Spuren von Enterocoelie zu finden, sind so gezwungen, dass man sie im Ernst nicht nehmen kann.

Dasselbe muss auch über die Coelomdivertikel gesagt werden, welche Van Beneden und Julin bei Clavellina beschreiben, weil die Höhlen dieser Divertikel bald verschwinden und das Mesoderm jederseits solide Zellenhaufen darstellt. Uebrigens konnte der spätere Untersucher des Gegenstandes—



Davidoff eben so wenig wie der frühere—Seeliger die Bilder auffinden wie sie van Beneden und Julin zur Annahme der Divertikel führten. Davidoff kommt in seiner Zeit zum Schlusse dass die Entstehung des Mesoderms bei Distalpia und Clavellina in keiner Weise an Ausstülpungen der Gastrulahöhle (Coelomdivertikel) gebunden ist, und dass die Mesodermentwicklung bei diesen Chordaten keineswegs auf eine den Hertwigschen Enterocoeliern entsprechende Form zurückgeführt werden kann (*loc. cit.* pag. 600 und 607). Da bei anderen Tunicaten bis jetzt keine Spur von Coelomdivertikeln gesehen wurden, so *beruht die ganze Coelomlehre, was die Chordaten betrifft, nur auf der Entwicklung des Amphioxus.* Da aber meine Untersuchungen gezeigt haben, dass auch beim Amphioxus diese Divertikel zur Leibeshöhle (Coelom) *nicht werden, sondern verschwinden*, so kann angenommen werden, dass ein wahrer Enterocoelion unter allen Chordaten nicht existiert.

It is very evident, then, that the coelom in Chordata is not archenteric in origin at all, and certainly cannot be homologised with the "archenteric outpouchings" in Echinodermata. This lacuna in the evidence for homologies has never been filled in; and even if it were, a still greater one remains. The "outpouchings" themselves in Chordata are not outpouchings of the *archenteron* but of the *deutenteron*; and the deutenteron (with its derivatives) is something characteristic of Chordata which has no counterpart whatever in Echinodermata.

The assumption which has been used to justify "the hypothesis that the mesoblastic somites of segmented animals are derived from a diploblastic coelenterate-like ancestor with folded gut walls," in the past, has been the belief that "the folding has arisen as a result of the necessity for an increase in the extent of the vegetative surfaces in a rapidly enlarging animal" (cf. Sedgwick, 1884).

Such a conception is entirely inadequate to explain either the embryological or the physiological facts. The *second phase* in development, which gives rise to the *segmented mechanisms*, teaches us that the distinctive factor in the differentiation of the higher segmented forms is the segmented nervous system and dependent upon it but coincidentally with it a segmented mesoderm (*vide* Kleinenberg).

The fundamental physiological distinction between the movements of animals without this segmental apparatus and those of creatures which possess it in even the crudest form was detected by Agassiz and Gould (1848) when they said:

The jelly fishes (Medusae) swim by contracting their umbrella-shaped bodies upon the water contained within and its resistance urges them forwards, ...others contract small portions of the body in succession which, being thereby rendered firmer, serve as points of resistance, against which the animal may strive, in urging the body forwards. The earth-worm whose body is composed of a series of rings united by muscles, and shutting more or less into each other, has only to close up the rings at one or more points to form a sort of fulcrum against which the rest of the body exerts itself in extending forwards.

It was this serial arrangement of successive rings (segmentation) which provided a point of departure from the peristaltic response of the nerve net system of lower forms. It depended upon a segmental autonomy in reflex



response—the reflex arc and the neurone of Waldeyer. In short, the achievement of a neuromuscular mechanism of segmental type has been the starting point in the production of forms invertebrate and vertebrate, endlessly diversified in type, all of which have solved in the characteristic segmental fashion the problem of orientating the body adequately with reference to its environment. Such forms, as I have shown elsewhere (*loc. cit.* 1922), proved especially capable in dealing with the problem of land progression. A segmented nervous system was therefore the initial event which led on the one hand to that pre-onychophoran form which was ancestor to Annelida, and on the other hand to the ancestor of Chordata.

It might be anticipated from these neurological and physiological considerations that an *ectodermal* origin of the segmented mesoderm is not only possible but highly probable. Huxley pointed out (1877) that the fundamental reason for the differentiation of ectoderm and endoderm was the physiological division of labour, providing in the first a tissue for *protection* and *locomotion* and in the second a tissue for *nutrition*. The segmental apparatus is first and foremost a *locomotor* tissue—for directive movement of the body as a whole. By second intention this mechanism of body movement is *protective*—i.e. for directive movement away from danger. Last of all, various portions of this system, so arising, become adapted in response to the demands of *nutrition*—i.e. the mastication and digestion of food, etc.; but such adaptations are rather final and not initial factors in the appearance and transformation of segmented mesoderm. It is for this reason that such segmented musculature as becomes secondarily adapted for mastication, deglutition, respiration, micturition, defaecation and parturition is amongst the most altered muscular tissue of the animal body and has preserved, with difficulty as it were, the traces of its primitive segmental simplicity and autonomy.

In consequence of these realities, histological criteria are available which support the *ectodermal* conception of the origin of the “deutenteric arch” (or “head process” or “dorsal plate”). The first criterion is that the cells arise at a definite site (the dorsal or anterior lip of the blastopore) and are progressively invaginated along the roof of the enteric canal—hence the “invagination” is real (cf. fig. 1). Secondly, this region of “ecto-mesoderm” is in a state of extraordinarily active mitosis while the definitive endoderm is relatively passive and amitotic. In consequence, there is a marked contrast between the anterior and posterior lips of the blastopore. Finally there is an intimate histological similarity (e.g. yolk content—*vide* Brauer) between the cells of the ectoderm and of the segmented mesoderm, while the cells of the ectoderm and the endoderm are in marked histological contrast.

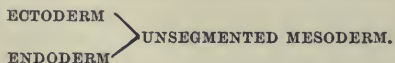
This invagination, from the ectoderm, of cells of different character from true endoderm cells was certainly recognised by the three British investigators, Balfour (1880–81), Scott (1882) and Shipley (1887). Indeed Shipley was revolutionary enough to state of *Petromyzon* that “its dorsal wall is composed of columnar cells resembling those of the general epiblast; the cells forming the floor have the same characters as the yolk cells.”

But Lwoff showed that identical conditions obtained through all Chordata and in this he has been confirmed, more especially by the admirable embryological researches of Brauer (1897). The revision of discordant views by Brauer is of the first importance. Moreover he has given support to Lwoff's view, by a careful study of the pigment content of the mesoderm (p. 457). The work of Lwoff and Brauer offers a better interpretation of the facts concerning the lower Chordata and has allowed of a direct homologisation of the process of mesoderm formation there with the process as followed by Amniota. Their points of disagreement from other workers are not points of fact but of interpretation. In this interpretation they have received noteworthy support from Carl Huber (1918), who has summarised the literature upon the subject, carried out a meticulous research upon the development of the mammalian chorda dorsalis and expressed himself finally as follows:

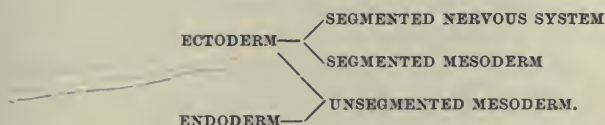
Since the endoderm takes no active part in the histogenesis of the head process, chordal canal and chordal plate and since the chordal plate becomes only partially and temporarily incorporated in the endoderm, there seems no justification for classing the chorda dorsalis as an endodermal derivative. And since the head process, the anlage of the chordal canal and derived structures, has its anlage in the cranial portion of the primitive node, a region of active ectodermal cell proliferation; and since the chordal canal and plate retain their continuity with the primitive node, which serves as a growth zone; there seems justification in regarding the head process—chordal canal and derived structures, chordal plate and chorda dorsalis—as a derivative of the ectoderm of the primitive streak region of the embryonic shield.

It is futile to embarrass chordate embryology with analogies which the science has long since outgrown. Not only the first but also the second postulate of Lwoff is justified—the justification not merely resting on a histogenetic basis but being confirmed by neurology, physiology and phylogeny. For just as Brachet (1921, p. 179) has insisted that the chorda dorsalis is a *neoformation* so, too, are the segmented mesoderm and neural tube that arise coincidentally with it. These *neoformations* are, as we have seen, the basis of the physiologist's *voluntary apparatus*; and it is rather to be expected that since this apparatus was designed to answer the call for *locomotion* of the body as a whole (Dart, *loc. cit.*) the stimulus behind segmentation was a more precise appreciation of environment by the ectoderm (Huxley) rather than some fortuitous internal expansion of the endoderm (Sedgwick). This conception is in entire agreement with the heterodoxy of Lwoff's derivation of the segmented mesoderm from the ectoderm in Chordata and with Kleinenberg's derivation of the segmented musculature and nervous system from a "gemeinsame Neuro-muskulanlage" in the ectoderm of segmented Invertebrata. It is expressed in the following scheme of classification:

*Coelenterata, Platyhelminthes, Nemathelminthes, Echinodermata, Mollusca.*





*Annelida, Arthropoda, Chordata.*

The traditional text-book pictures founded upon Hatschek's figures of *Amphioxus*, and an imperfect conception of the nature of the segmented mesoderm, are misleading. The fact of bilateral symmetry in this mesoderm so impressively represented in Hatschek's figures is undoubtedly valuable; but the equally fundamental truth revealed by this series of investigators is thereby lost; namely, that the whole segmented mesodermal mass is an "invagination" of the ectodermal anterior lip of the blastopore.

Meantime a wholly different series of investigators including Kastschenko (1888), Goronowitsch (1892), Miss Platt (1893), etc.—as Landacre (1921) has shown in his admirable summary—have declared that much of the "head mesoderm" is proliferated from the ectoderm directly—a fact which has ultimately received important experimental confirmation in the work of Stone (1921).

This "head mesoderm," so arising, is part of the segmental mesoderm—it gives rise to the "trabeculae, Meckel's cartilage, the palatoquadrate and all of the branchial cartilages except the second basi-branchial or urohyal" (according to Landacre). It would, indeed, have been an extraordinary fact if this mesoderm had been ectodermal and the mesoderm giving rise to the segmental musculature had not been ectodermal (as so many have maintained).

The cumulative evidence of the two series of observers mentioned, has shown that not only the so-called "head mesoderm" but also the segmented mesoderm of the trunk is primarily ectodermal; so the two together form an indivisible harmonic structural unity.

This unity in character is illustrated not only by the embryological evidence adduced. We have already recognised that the whole of the striated (mesodermal) musculature (derived from the deutenteric arch formation) is to be contrasted with all other unstriated (or dermal) musculature, because the dermal (unstriated) musculature is innervated by the sympathetic (nerve-net) system only, whereas the true mesodermal (striated) musculature is innervated by the sympathetic system and by the central nervous system as well. In this fundamental fact of double innervation we recognise the *unity* of the adult tissues derived from the deutenteric arch formation and appreciate in addition that we have, in this tissue, an evolutionary advance on the dermal musculature which was there before it—that the mesodermal musculature, as a whole, is a new formation.

It is equally significant that from the striated musculature there flow continuously into the medullary tube those impulses of "muscle sense" and "tendon sense" which provide the organism with information concerning its



location in space. This property of the mesodermal (striated) musculature, which is unknown in the dermal (unstriated) musculature, is at one and the same time a token of its separation from the (endoderm) tissues which possess only an "enteroceptive" quality and its affinity with the tissues (ectodermal only) which possess the "exteroceptive" quality so preponderantly. Unfortunately these terms "extero-, proprio-, and enteroceptive" have meaning only in neurology—as denoting the different kinds of afferent impulses recognised in the animal body. The terms have had no morphological meaning hitherto, nor is it suggested here that they should be given a morphological meaning. Attention is merely drawn to the fact that the distinctions in the "afferent" system, inculcated by Sherrington, have as their morphological foundation one fundamental fact and one only: that the enteroceptive impulses are mediated primarily by a nerve-net (vegetative) nervous system, the exteroceptive and proprioceptive primarily by a segmented (central) nervous system; the former is initially the chaos of a network, the latter the order of serial arrangement.

This serial segmental arrangement is found in the ectoderm and it is found in a certain restricted portion of the mesoderm. It has never been found in the endoderm of any organism. Are we then to attribute to this endodermal parent, fertile as she has been, such an unnatural offspring?

But the unity in character, or better the maternal-filial relationship between the ectoderm and the segmented mesoderm is equally patent if we consider the other derivative of the deutenteric arch (or dorsal plate). I refer to the skeletal parts, the bones, the fulcra and points of attachment upon which the segmented musculature acts. The most exacting histological observation by observers of all nationalities over a long period of time has only served to reveal the intimacy of the homology between the various processes of bone formation in the ectoderm and in the segmented mesoderm, whether the end results be scales, the so-called "dermal" bone, "cartilage" bone, or "membrane" bone. What evidence have we that the endoderm preserved the faculty to produce such structures itself, much less to produce a whole sheet of body tissue which should give rise to such structures at a considerably later period of evolutionary history? In other words the tissues to which this sheet of invaginated ectoderm gives rise vindicate their ancestry by their close histological resemblance to similar tissues whose origin from the ectoderm is indisputable; and so the whole *segmented mechanism of musculature and skeletal parts* manifests in its lineaments (embryonic or adult) that it sprang from the same womb—twin births as it were—which gave origin to the tissue controlling its activities, namely, the *segmented medullary tube*. It is by these criteria of histology and of neuro-physiology as well as, or rather, in preference to those other hypothetical and very erroneous criteria of echinoderm comparison, that these questions should be examined and an answer returned.

Superficially, the recognition of this fact of ectodermal invagination might seem to be merely a verbal quibble; but actually it is a generalisation of the

greatest significance not only for physiology, neurology and embryology, but for all orientation and consequently for all descriptive morphology, whether of the skeletal, osseous or nervous systems—indeed of the whole body. Because orientation is of such paramount importance in descriptive morphology I wish to examine, in the light of the information gathered concerning the segmented mesoderm, two ancient questions of orientation.

#### THE ANTERIOR END OF THE BODY

In this fact of the second phase of invagination we have the ontogenetic repetition of a fundamental incident in phylogenetic history, namely, that the segmental tissues were introduced into the framework of a creature which previously had no segmentation at all but already possessed a mouth and an anus. Since the segmental tissues are the tissues of directive movement, this is only another way of saying that the creature understood how to deal with food before it appreciated how to seek for it.

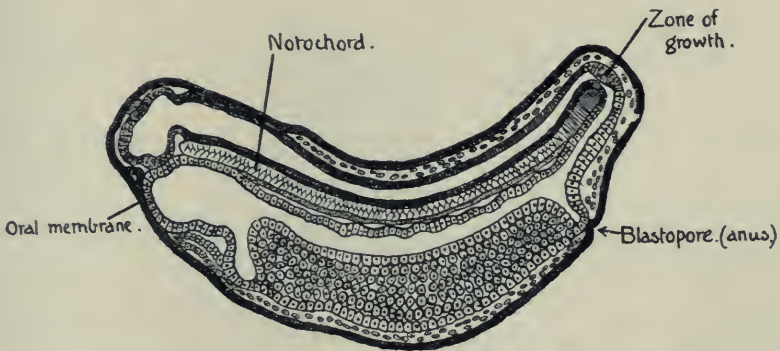


Fig. 2 (after Goette) for comparison of "head" and "tail" growth.

Whether we agree with those who (like Sedgwick and O. Hertwig) derive the mouth from the division of the blastoporal slit, or, with those (like Huxley) who postulate for its production a new formation, we must recognise the general admission that the laying down of these segmental tissues has taken place along a central linear axis extending between these two sites. The proof of this statement lies in the fact that, when the ectodermal invagination has given rise later to the segmented tissues, the segmental tissues ("le dos entier de l'embryon") are limited in front and behind respectively by these two sites (oral and anal membranes). This fact is picturesquely emphasised by a comparison of the behaviour of the segmental tissues posteriorly and anteriorly during development.

Fig. 2 is a schematic sagittal section of *Bombinator igneus* (after Goette) to illustrate the changes which take place after the invagination (pictured for another amphibian in fig. 1). The original blastoporal site is now represented, as is well known, by the anus. The zone of growth still lies (morphologically

speaking) anterior to the blastopore (anus), and gives rise to the segmented tissues of the tail. Under it lies the neurenteric canal; dorsally, the canal opens into the neural tube and ventrally into the post-anal gut. At this stage the "deutenteric arch" is no longer exposed in the gut cavity but has become separated from it by the undergrowth of true endoderm and has itself become differentiated into notochordal and somitic tissues. Concerning the relation of the tail to the anus Brachet (p. 255) has suitably summarised our present information:

Quant à la queue, elle procède de l'allongement et de la différenciation du bourgeon caudal. Elle surplombe d'abord l'anus, puis le dépasse d'avant en arrière. Par définition, elle est, non seulement chez tous les Amphibiens, mais chez tous les Vertébrés, la portion postanale de la larve. Or l'anus étant, par son origine même, l'extrémité terminale de la partie ventrale du corps, il s'ensuit que le bourgeon caudal n'est qu'un prolongement de sa partie dorsale et ne contiendra dans sa substance que le système nerveux central, la chorde, les parties juxtachordales du mésoblaste et la voûte du tube digestif.

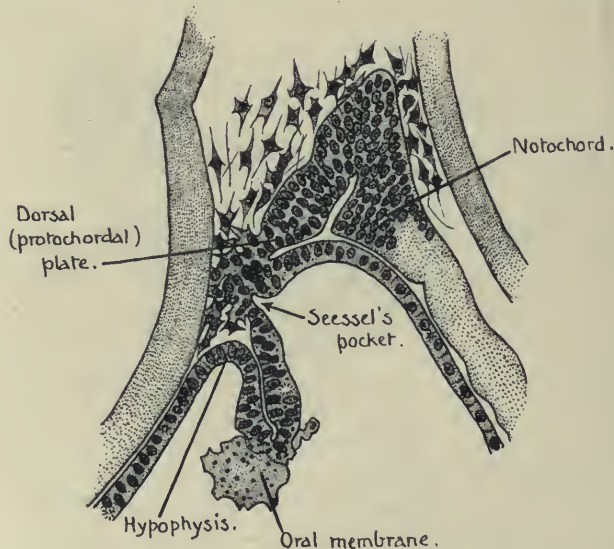


Fig. 3 (after Bonnet) to show anterior end of the dorsal plate (deutenteric arch).

Now, no embryologist would seriously put forward the notion that the tip of the tail or the posterior termination of the central nervous system in the filum terminale represents the morphologically terminal end of the chordate body. It is equally impossible to regard the projecting tip of the snout, much less any supposed termination of the neural tube, as the true anterior end of the body as has been done by Hatschek (1909) and others.

Fig. 3 (a sagittal section of a dog embryo after Bonnet) presents a certain stage in the development of the anterior region of the body. The oral membrane *O*, hypophysis *H*, and Seessel's pocket *S*, present a fixed and striking



relationship with one another. The "voûte deutenterique" of Brachet is represented anterior to the notochord *N* by the so-called "prae-chordal Platte" of Oppel ("protochordal plate" of other authors). The continuity of this structure with the notochord and the direct part it plays (cf. K. M. Parker, 1917) in the production of the anterior head cavities and in consequence (cf. E. A. Fraser, 1915) of the eye musculature show its continuity with and genetic relationship to the "dorsale Einstülpung" of Goette (i.e. the "dorsale Platte" of Lwoff), which gives rise throughout Chordata to the axial skeleton and the segmented mesodermal tissues generally.

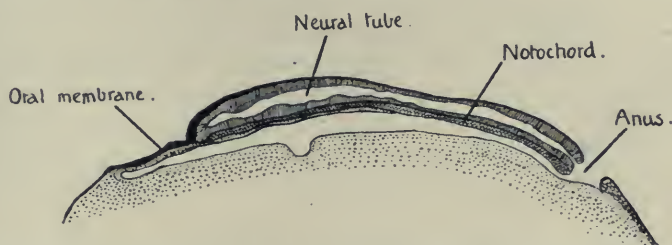


Fig. 4 (after Brauer) to emphasise the linear morphological orientation of the segmented tissues between the oral membrane and anus.

Reference to fig. 4, taken from the work of Brauer, will make these facts obvious. We must recognise that, as far as the head is concerned, it develops by a lengthening out of the neural tube and the segmented mesoderm headwards over the oral plate which is directly comparable with the prolongation of these structures tailwards beyond the anus. Just as the prolongation of these structures posteriorly causes a dorsal diverticular extension of the gut to form the post-anal gut, so their *anterior prolongation* is the causative factor in the production anteriorly of the dorsal diverticular extension of the gut known as Seessel's pouch or pre-oral gut. Subsequently, just as the post-anal gut disappears in ontogeny so the pre-oral endoderm "does not play any part in later development" (K. M. Parker, 1917, p. 195).

It follows from these facts that the caenogenetic tissue of the protochordal plate and its derivatives ends in the vicinity of Seessel's pocket and that the protochordal plate is *morphologically entirely posterior to the oral membrane* just as the same tissue is morphologically entirely anterior to the anal membrane. Consequently the so-called prae-oral gut is morphologically *post-oral* and the post-anal gut is *prae-anal*. Finally, the most valuable morphological antero-posterior orientation which we possess for all Chordata is the oral plate-anal membrane orientation; and the oral membrane is the true anterior end of the chordate body.

The criterion of antero-posterior orientation so established needs a word of comment because *the vertebrate mouth* has been provocative of such extraordinary speculations. Even at the present time we find some investigators (e.g. Neal, 1921), who hold that "the present vertebrate mouth may be con-

sidered as the third—or fourth, if the neuropore be added—mouth in chordate cephalogenesis.”

The contribution of Beard (1888) has done much to eliminate the crudities of the earlier speculations of Dohrn, Owen, J. T. Cunningham, and others concerning the fourth ventricle, infundibulum and other routes which the “palaeostoma” was supposed to have taken. At the same time Beard’s own speculation concerning the hypophyseal “palaeostoma” is scarcely happier. Ontogeny provides no evidence whatever to support a “palaeostoma” other than the *oral membrane* itself.

From such bizarre interpretations it is refreshing to turn to the single postulate which Huxley (1877) regarded as sufficient to account for the appearance of a *stoma* in animals above Coelenterata, namely “the development of a secondary aperture near the anterior end of the body, which becomes the permanent mouth.” The only modification of this conception suggested here is that this secondary aperture was not merely *near* the anterior end of the body, but was itself *the actual anterior end*.

#### THE ANTERIOR END OF THE NEURAL TUBE.

The recognition of the “second phase” in chordate development has further a most important bearing upon the problem of the anterior end of the neural tube. We have recognised as one of the constituent portions of “le dos entier de l’embryon” the *neural tube* itself. In direct consequence of this fact, the one and only point where the neural plate and axial mesoderm (the coincident phylogenetic new formations) come into most intimate relationship with one another, and at the same time with the ectoderm (hypophyseal inpocketing) and the endoderm (Seessel’s pocket) which they are separating—this point is at the anterior end of both the neural plate and of the axial mesoderm. This site, common to all these structures, may be termed the *infundibular* point, and the infundibular recess, which is in most intimate contact with this site, is to be regarded as the anterior extremity of the neural tube.

It is generally laid to the credit of His that he was the first to differentiate clearly between an alar and a basal lamina of the neural tube and to give a clear and precise statement of the development of that structure, placing the anterior end of the neural tube in the *recessus infundibuli*.

As a matter of actual fact, von Baer (1828) had pointed out many years before, against the teaching then current, that “der hohle Cylinder (i.e. the neural canal) bestünde aus zwei ursprünglich vereinigten Hälften.” He showed (S. 64) that “Jede Seitenhälfte des Rückenmarkes ist durch eine mittlere helle Furche in einen obern und einen untern Strang getheilt” and from considerations of primary position and subsequent growth had already termed the infundibulum “das wahre ursprüngliche Ende vom Centraltheile des Nervensystems.”

Various authors since the time of von Baer, however varied their line of approach, have been led to identical or approximately identical views. The

outstanding features in regard to the infundibular location is its *fixity* from the embryological and osteological point of view. Thus J. E. Frazer (1921) states:

Some years ago (*Lancet*, 1916) I described the pituitary region of the brain as the most *fixed* place within the skull, and referred the formation of the midbrain-flexure to the forward growth of the hind-brain acting against this *fixed point*....The definite adhesion of stomodaeal and neural ectoderm at this place, and their association with the upper end of the bucco-pharyngeal membrane, Seessel's pocket (when present), and the adherent notochord, seem to me to give a guarantee of *fixation*, supported by every sagittal section, which must influence the shape of a brain growing up against its *fixation* here. The brain growing more rapidly than the skull-base, piles itself up into curves, so to speak, and these then owe their existence mechanically, and at least in part, to this *fixation* of the forebrain.

Equally definite is the dictum of Sir Arthur Keith (Keith and Campion, 1921) in the following excerpt:

The superimposition has been made so that pituitary fossa falls on pituitary fossa, and cribriform plate on cribriform plate, because a prolonged experience has shown one of us (A. K.) that the pituitary or sphenoid region serves best as a *fixed point* in comparing the development of one skull with that of another. Similarly Brachet (1921) in discussing the development of the brain expresses himself (p. 333):

Comme celle-ci est *fixée* à ses deux extrémités, en avant par l'hypophyse et la bouche, en arrière par sa continuité avec le tronc, elle est obligée de se soulever en une voussure proéminente, qui surplombe et dépasse de plus en plus la région de la membrane pharyngienne.

That the cranial flexures are a measurable sign of the degree of twisting that has taken place about the end of the notochord is well recognised. Hertwig (p. 425, Mark's translation) states:

The extent of these curvatures is very different in the various classes of vertebrates. Thus the cephalic flexure is only slightly emphasised in the lower vertebrates (Cyclostomes, Fishes, Amphibia); it is, on the contrary, much greater in reptiles, birds and mammals; but in Man especially, whose brain is most voluminous, all of the flexures are developed to a very high degree.

This *fixity* is the *conditio sine qua non* of any landmark and these weighty statements, representing the results of experienced observation, are corroborative of von Baer's view. They might be expected sufficiently to solve the problem which we have here engaged, but it is necessary to examine closely other views which have been advanced at different times over an extensive period and which lay claim to being more adequate interpretations of the evidence.

This evidence, gleaned from the study of the ontogeny of the chordate neural tube, has given the most diverse results in the hands of various workers.

His (1893) regarded the anterior end of the neural tube as closing during development by a process of conerescence, which extends from the infundibulum forwards to the upper edge of the lamina terminalis. Consequently,



although His did place the extreme anterior end in the *recessus infundibuli*, he gave no morphological reason for so doing.

Von Kupffer (1893) chose the *recessus neuroporicus* at the upper edge of the lamina terminalis, but Keibel (1889), J. B. Johnston (1909) and others have selected the *optic chiasma* as the point in question. It is evident that by means of the "raphe" conception His was able to bring his views more or less closely in line with von Kupffer's notion of the neuropore and yet to state that he differed from Keibel's optic chiasma "nur um wenigens."

But this rhetorical treatment of the matter is unsatisfactory, unscientific and inadmissible. We will discuss the two points in turn considering the claims, first, of the neuropore; and, second, of the optic chiasma.

#### *Neuroporic recess.*

Von Kupffer put forward in various papers a series of postulates which have not received corroboration: (1) that the last point of closure of the neural tube and its separation from the ectoderm is constant for Vertebrata and is marked in the adult by the recessus neuroporicus; (2) that the point in question is homologous with the "neuropore" of Amphioxus; and (3) it is homologous also with the "lobus olfactorius impar" in Cyclostomi.

In the first place, as regards the lamprey homology, Kappers (1921) has said quite recently that von Kupffer's point (neuropore) loses much of its importance because of Woerdeman's (1914) demonstration that the olfactory placode is in contact with the "Vorraum" of the hypophysis. But quite apart from any embryological demonstrations at all, it is clear that the homology of the unpaired olfactory lobe of Cyclostomes with the embryonic neuropore of vertebrates by von Kupffer is pure speculation; for it is inconceivable how any homology of a cavity with a definite cellular mass can be contemplated. The only homology the *lobus olfactorius impar* can have is with the paired lobes of higher forms. As Karl Peter (1906) pointed out (Hertwig's *Entwickelungslehre*) nobody has ever confirmed von Kupffer's "triple" origin of the olfactory organ in Cyclostomes nor his unpaired olfactory nerve passing to the unpaired groove.

In the second place, Hatschek (1909) by a comparative study of *Petromyzon* and *Amphioxus* has dealt with von Kupffer's second contention. He has refuted his homology of the neuropore of *Amphioxus* with the structure, so-named, in other Chordata and has insisted upon the "roof" position of the lamina terminalis and associated structures.

Finally, other investigators have rendered yeoman service to embryology and neurology by a critical examination of the first and really basal postulate in von Kupffer's thesis. Koltzoff (1902), by a study of the development of the ammocoete larva of *Petromyzon*, showed that the "neuropore" of von Kupffer is not the terminal point of the neural tube at all but can be regarded at best as merely that place where the neural tube last loses contact with the ectoderm. He further insisted that the "recessus opticus" belongs to the dorsal

or roof structures of the neural tube and that in later stages the apex of the *infundibulum* serves as the boundary mark between the floor and roof of the neural tube. In this way, he urged, the floor of the tube lies in contact with the notochord, the roof with the ectoderm.

Equally vigorous is the attack of Fanny Fuchs (1907-8) upon the speculations of von Kupffer. The latter had assumed, as stated previously, that the last point of separation of the neural tube in ontogeny is represented in the adult by the *recessus neuroporicus* and that it constitutes the most anterior point of the brain in all Chordata. Of this Fanny Fuchs (1907-8) has said:

Dieser Zusammenhang (of brain and ectoderm)...kann bleiben erhalten länger an irgend einer Stelle. Der Prozess der Ablösung des Hirns vom Ektoderm geht wohl etwa von der Mitte des Gehirns aus und schreitet von da nach vorn und hinten fort, so dass schliesslich irgendwo in der Nahe des vorderen Hirnendes dieser letzte Zusammenhang bestehen bleibt. Ebensowenig aber, wie die Stelle genau zu fixieren ist, wo die Ablösung beginnt, ist auch die, wo sie aufhört, als fester Punkt zu betrachten, der im allen Hirnen an der gleichen Stelle liegt. Offenbar wird diese Stelle wesentlich durch die Formbildung des Hirns bestimmt; sie wird immer da liegen, wo die geringsten Veränderungen durch Wachstum vor sich gegangen sind.

Daraus geht schon hervor, dass der Neuroporus nie an der stark wachsenden Vorderseite des Hirns (*lamina terminalis*), sondern höchstens an ihrem obern Rande liegen kann. Dort wird er auch sehr häufig angetroffen, wie ein Blick auf v. Kupffer's Medianschnitte zeigt (Selachier, Ganoiden). Bei den Anuren aber liegt er viel weiter hinten, etwas vor der vorderen Grenze des Mittelhirns.

Aus dem Gesagten geht wohl zur Genüge hervor, dass die Stelle, wo der Neuroporus liegt, *wechselt* und dass sie niemals an der Vorderseite des Gehirns, sondern immer an seiner Oberseite liegt.

That this important statement of Fuchs is not captious but well-grounded has been amply shown by the still more recent embryological researches of Schulte and Tilney (1915). In a careful study of successive stages of development in the domestic cat these authors found that:

the neural folds first meet in the region of the future mesencephalon but the closure is not simply progressive from this point in both directions. On the contrary it is incident simultaneously at several points which may be rather widely separated. In the eight-somite embryo, in addition to the closure of the mid-brain, which extends from the optic anlage to the quintal ganglion, there is a second closure between the quintal and acoustico-facial anlagen; and again, after an interval at a third point the folds seem on the verge of meeting. There is also some fusion cephalad at the ventral margin of the neuropore. This is of some theoretical importance and diminishes the significance of the neuropore as a morphologic landmark.

The discussion of this point by these authors is worth quoting *in extenso*.

To accept the last point of attachment of the ectoderm marked by the *recessus neuroporicus* as the extremity of the axis, implies that the raphe below this point is a suture between the basal plates;...further it would seem the necessary consequence of the acceptance of this landmark (*recessus neuroporicus*) that the mammillary and infundibular regions and the ventral half of the

optic vesicles themselves were derived from the basal laminae. To accept the recessus neuroporicus as the ontogenetic pole of the brain seems, therefore, to disregard the ventral deflection of the neuraxis and the composition of the wall of basal and alar plates.

It is clear, then, that every single one of the postulates of von Kupffer has proved decidedly unsatisfactory and that the neuropore, which *changes* and has *no* homologies of the type suggested cannot be regarded seriously as a morphological landmark. The vast amount of detailed comparative embryological research which they have elicited has failed entirely to ratify his original conceptions.

#### *Optic chiasma.*

It should be called to mind, in the first place, that the traditional arrangement of the olfactory nerve, as the first, and the optic nerve, as the second cranial nerve respectively has not always remained uncontested. Thus, Mrs Susanna Phelps Gage (1905), assuming the infundibulum to be the anterior end of the neural tube, insisted that the position of the chiasma denoted that the eyes were the *first* pair of the segmented organs unless the infundibular organs of Boeke (1901-2) precede them in the series. In this respect Mrs Gage has not been alone, for van Wijhe (1882) suggested "Da der Olfactorius vor der Entstehungsstelle des Opticus auftritt, ist er zwar scheinbar der vorderste, in Wirklichkeit aber der zweite (nicht segmentale) Kopfnerv"; and again he states, "Der Opticus ist morphogenetisch der vorderste Hirnnerv, der Olfactorius der zweite." With this conception Hatschek (1909) concurs and so, logically, should all who, like Keibel (1889), Johnston (1909) and Kingsbury (1920-21) believe that the optic chiasma is the true anterior end of the neural tube. Sedgwick certainly upheld this view (*Encyclopaedia Britannica*) as recently as 1911.

The complete discussion of the evidence against such a reversal of the age-honoured sequence of cranial nerves would lead us far from the central issues of this thesis, but several comparative anatomical facts make its acceptance impossible. In the first place, the optic chiasma cannot be used as a fixed morphological landmark since, like the neuropore, it is in "no way constant" and is sometimes situated *entirely anterior to the corpora striata*. As Victor Franz (1912) has stated, "Mit Kappers und frühern Autoren mache ich noch darauf Aufmerksam, dass das Chiasma nervorum opticum keineswegs konstant an einer und derselben Stelle liegt, sondern bei manchen Arten (*Gadus*) sogar bis oral von den Lobi anteriores verschoben ist."

It is impossible to regard any structure which has this degree of variability as a point of morphological value. In the second place attention must be drawn to the discovery which Nils Holmgren (1918) has made recently in certain bony fishes and which he calls "ein Kuriosum." That it is no mere curiosity of spasmodic occurrence is shown by its repetition in *Osmerus*, *Cottus*, *Perca*, etc. (cf. Nils Holmgren, 1902). This "Kuriosum" is the fact that the *nervus ter-*



*minalis* and the *nervus olfactorius* utilise the optic tract as portion of their sensorial distribution through the medium of the so-called terminalis-opticus and olfacto-opticus tracts. These tracts, according to Holmgren, form an appreciable part of the so-called "efferent" fibres of the optic tract.

Many years ago Edinger pointed out that the so-called "olfactory field" and the thalamencephalon is "completely covered laterally through the great fibre system of the optic tract" and it has been generally recognised (e.g. Judson Herrick, 1908) that "functionally and genetically, the retinae, optic nerves, chiasma and tracts and the optic thalamus (*sensu stricto*) should be associated with the optic tectum of the mid-brain to form an *ophthalmencephalon* whose boundaries cross freely those of the classic encephalic regions." Indeed, so clearly is this embracing relationship of the optic tract to the prosencephalon recognised nowadays that Kappers has insisted on terming the habenular commissure—which is the most posteriorly situated structure of this "embraced" area—"telencephalic." ■

This placing of a large portion of the telencephalon posterior to the chiasma and the embracing relationship of the *ophthalmencephalon* to the telencephalon form one of the most intricate puzzles in neurology. But the facts, viz. the embracing relationship of the *ophthalmencephalon* (Edinger, Herrick) and the variable position of the chiasma in certain fishes (Franz, Kappers and others), the absence of any decussation whatever in lowly forms like *Myxine* (Harris and Parsons) are only to be explained by the assumption that the optic tract, in the higher Vertebrata, has actually undergone much shifting from the primitive situation of its constituent elements; and further, that the extent of this shifting and the degree of chiasmatic formation itself has been very variable in different Vertebrata, particularly amongst Fishes.

The external situation of the eyes themselves is capable of extensive migration, in ontogeny, in fish of certain families (e.g. sole and plaice). Such migrations of the peripheral optic apparatus, in ontogeny, prepare us to expect that extensive and very varied modifications of the central or receptive apparatus were attempted before the successful chiasmatic solution was achieved. The optic chiasma was not "created."

The researches of Holmgren, which have revealed hitherto unrecognised components of the optic tract, indicate the probable lines along which the modifications in structure proceeded to give rise finally to the optic chiasma. Presumably the original *sensorium* for the sense of sight was simply restricted to a segment of the neural tube lying posterior to the olfactory (and terminal) segment. Its original site may be most reasonably regarded as that now occupied by the tectum opticum. Forward growth of a portion of the optic sensorium (i.e. of the optic tract itself) in phylogeny would entail to external appearance the embracing of the olfactory field by the *ophthalmencephalon*, and in actual fact, the involvement of the optic sensorium (optic tract) with the sensorium of the olfactory (and terminal) nerve (*tractus terminalis-opticus* and *tractus olfacto-opticus*). The involvement of the optic tract with this

primitive sensorium, now so intimate as to be apparently inextricable, can be rationally explained by this conception of a forward migration in phylogeny not only of the eyes but also of their sensoria.

The forward migration of the optic sensoria to form the optic chiasma did not occur in such a way that the ophthalmencephalon embraced the whole *vertical height of the neural tube*, but in such a way that the ophthalmencephalon became incorporated with the olfactory (and terminal) sensorial tissue (alar lamina of His) which primitively lay anterior to (not vertical to) it. Thus, whatever be our criterion of the anterior end of the neural tube, the caenogenetic and migrating optic chiasma is a will-o'-the-wisp the pursuit of which will merely serve to entangle neurologists in a mental morass just as long as embryology remains unchecked by the findings of comparative anatomy.

Considerations of the distribution of the histological architecture of their respective sensoria teach us therefore that the optic nerve is morphologically posterior to the olfactory nerve, and that the olfactory nerves precede the optic nerves in the segmental series suggested by Mrs Gage. It should not be surprising either, that the involved series of changes which has obviously taken place in this difficult region to produce the optic chiasma should have been productive of a developmental picture (*repli cerebral transverse* of Brachet) which has too frequently defied the interpretations of embryologists who fail to take account of the same facts of comparative anatomy and neurology.

The chiasma is caenogenetic and the olfactory (and terminal) apparatus lies more anteriorly. So the olfactory apparatus must be the most anterior of all chordate sense organs unless Boeke (1913) is correct in believing that the ancestral vertebrate had paired infundibular organs such as certain larval fishes ordinarily possess. Relying upon Boeke's evidence, Mrs Gage (1905) has already suggested that the infundibular organs are the first in the segmental series of sensory mechanisms in Chordata. This line of evidence, therefore, if valid, corroborates the ancient conclusion of von Baer (and the identical one of Keith, Frazer, and many others) that the infundibular region is the most anterior and most fixed portion of the neural tube.

Certain other investigators have attempted to provide evidence towards a solution of this problem of the anterior end of the neural tube by a histological testing of the hypothetical brain morphology advanced by His. His interpreted the facts elucidated by von Baer as demonstrating an early subdivision of the neural tube into motor (basal) and sensory (alar) laminae. Consequently these observers have examined the anterior parts of the neural tube histologically to find the anterior termination of this ventral lamina (or column).

Tretjakoff (1909), by examination of the brain of *Ammocoetes*, showed that in front of the infundibulum there does not exist a single primary "effector" element in the neural tube; in short, that the whole of this region, topographically anterior to the infundibulum in the adult, is entirely set apart for "receptor" and "association" functions. In his later work, Tretjakoff



(1913) pointed out further that the researches of Boeke, Kappers, Dammerman and others bore out his own contentions that the infundibulum itself was a receptor mechanism and so reinforced his central argument that the whole of the region anterior to it in the adult was "alar" in type, and therefore was morphologically posterior to the infundibulum (on His's own hypothesis).

But the subsequent investigation of mammalian forms by Malone (1910 and 1914) has clinched this type of evidence concerning this region for all vertebrates by showing that even in such advanced forms "the basal optic ganglion, the nuclei tuberis lateralis, nucleus paraventricularis and the nucleus tubero-mammillaris are composed of cells whose histological character indicates that they are not efferent, but are concerned in *receiving* and *correlating* incoming impulses; these cells do not possess the relatively large, diverse Nissl bodies characteristic of efferent cells."

It needs no detailed logic to demonstrate that this "laminar" criterion of His, and those who follow him, is entirely contradictory of his previous criterion of the "raphe" as the anterior limit. If this sensory-motor subdivision of the neural tube, adopted by His, were regarded as the criterion for determining the point in question not only the neuropore but the optic chiasma, the whole "raphe," and even the infundibulum itself are worthless as anterior landmarks. To accept the His doctrine in its entirety is impossible—either his "raphe" or his "laminae" must succumb.

These facts have been brought out to some extent in the recent contribution to the question by Kingsbury (*loc. cit.*), who has given us an original interpretation of the His morphology. Still, there is no reason why our morphological views should be handicapped in any way by the "laminar" conception attributed to His. It has value as a generalisation, through the pioneering work of Bell and Waller, but should not be conceived any longer in the sense originally intended by His.

Moreover, in collaboration with Dr Shellshear, I have recently put forward the conception (1920-21) that the motor neuroblasts are developed extra-neurally, i.e. outside the neural tube, and are subsequently incorporated within it during ontogeny. If this conception is correct—and a very large body of facts supports it—the so-called *motor* or basal lamina of the neural tube only achieves that significance secondarily. The neural tube is primarily merely a coordinating mechanism composed of *intercalated* elements. To find the infundibulum composed of these elements does not destroy its title to being the anterior end upon our hypothesis; it would destroy that title upon the hypothesis of His. But quite apart from this discussion the motor "column" of nuclei has long been recognised as a segmentally repeated succession of cell-groups—groups which are widely separated particularly in the intracranial part of the neural tube. They form no true *column* at all and do not end at any well-defined morphological point. This quasi-"column," since it lacks continuity, can scarcely be used as defining the true anterior end of the neural tube.



Although the motor "column" has no importance in deciding the question positively, it does have great significance in supplying certain negative information, namely, that the anterior end of the neural tube, wherever it lies, is certainly *not behind* any motor cell group in the tube. Kingsbury (*loc. cit.*) has recently put forward the suggestion that the anterior end of the floor-plate of His lies a great distance posteriorly to the infundibulum and posteriorly to the oculo-motor nucleus. Creditable as is any attempt to introduce accord where so much discord has been apparent the suggestion advanced by Kingsbury is entirely retrograde. It is impossible to regard a point located at the junction of the mesencephalon with the metencephalon as the anterior end of the neural tube.

If, however, we retain the division of the neural tube which von Baer first suggested (and His later adopted) and appreciate that the "sensory-motor" lamination has no morphological significance (save the indirect one above referred to) it is possible, for argument's sake, to let the sulcus terminalis end in the infundibular recess (where von Baer regarded it as ending) and not in the optic recess (where Johnston and others would have it end), nor in any other later out-pouching of the neural tube, such as the cerebral vesicle itself (where one might just as reasonably regard it as ending).

If we retain this subdivision of the tube and this termination of the sulcus terminalis, then the "raphe" of His would meet the ventral laminae and the floor-plate of His in the infundibular recess; the infundibular recess would be recognised for the true anterior end of the neural tube and the whole district of the "raphe" from infundibulum to neuropore would be recognised for the roof which von Baer, Hatschek, Tretjakoff, Malone, and so many others have recognised it to be.

#### CONCLUSIONS.

Most of the discord revealed by a study of the literature of the last two decades is due to the fact that the question of the anterior end of the *neural tube* has been approached without regard to that other most significant issue—the anterior end of the *body*. Consequently the selection of the point in question has been arbitrary in practically every case, while collectively the results obtained have been highly conflicting.

The internal evidence reveals the fallacy of accepting any of the criteria hitherto suggested. The *neuropore* has been found to be incapable of true demonstration or homologisation. The *optic chiasma*, as a landmark, rests on equally unsatisfactory foundations. The "*laminar*" conception has not ratified any point hitherto taken and, in the nature of things, is incapable of doing so.

If we go back to first principles we will recognise that the segmented neural tube is only as old as the segmented skeletal and muscular systems. These phylogenetically coincident mechanisms are distinctive of the Chordata—their most obtrusive characteristic. There is but one single point—the only point not in conflict with the evidence of comparative neurology and ontogeny, and corroborated by teratology and osteology—which lies morphologically

at the anterior end of all of these segmented systems. Lying morphologically posterior to the oral membrane (the anterior end of the body), this site is simultaneously the anterior end of the axial mesoderm and of the neural tube. It is the infundibular point.

It is from this *fixed* point that the brain, when it became expanded, was prolonged forwards and so caused its already fused roof to face ventrally. Thus the district lying between the infundibulum and the lamina terminalis (including the chiasma) faces ventrally in most vertebrata. But this ventral "facing" of structures originally dorsal is no novelty in cerebral morphology. We do not hesitate to regard the cerebrum or cerebellum as expansions of the alar (sensory) folds, when considerable areas thereof are exposed ventrally.

It is from behind this same *fixed* point that the mesodermal rudiments of striated muscles have slipped laterally and have been thrust forwards to give rise to the eye musculature, jaw musculature, etc., and it is from ectoderm lying morphologically posterior to the oral membrane (and because of their juxtaposition posterior to the infundibular point) that "mesoderm" has been derived, which sank under the ectoderm, and provided on the one hand encapsulations for various specified areas of the expanding neural tube and the sense organs connected with it, and on the other hand, sites of attachment for the already mentioned musculature. Hence the trabeculae, the cartilages of the sense organs of the skull and the branchial arches (however far forwards or ventrally they may become displaced) have arisen from tissue entirely posterior to the oral membrane and posterior to the infundibular point.

Many arguments might be urged in demonstration of this statement but, after all, they are all implicit, in some form or other, in the embryological and anatomical data which we have already considered, and further discussion would merely serve to swell unnecessarily the size of the present article. I shall merely state, in conclusion, that I do not know of a single new fact or observation amongst those which I have here brought forward, nor have I attempted to bolster up my argument with a single new picture or diagram. On the contrary, it has been my object to utilise as widely as was convenient, within the limits of a brief article, the most diverse discoveries of a long series of distinguished observers, whose statements are the more compelling because they have no prejudice; reckoning it a happy and worthy service if it should fall to my lot merely to show that these diverse discoveries, in so many spheres of investigation, were pertinent to the difficult problem in hand and afforded simultaneously the same answer.

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# ON THE HAIR SLOPE IN THE FRONTAL REGION OF MAN

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IN the following paper I intend to deal with the results of an investigation upon the direction of the hair in a circumscribed region of the skin, viz. the forehead. Some observations on this phenomenon, made casually in the course of a methodical research on the development of the human face, convinced me not only of the incompleteness, but also of the inaccuracy of previous descriptions.

This conviction induced me to extend our knowledge on this subject and I therefore examined the hair slope in the frontal region of a large number of human embryos. This investigation was very instructive. There is surely no other region of the human skin with so great a variability of the hair streams as the frontal region. The cause of this seems to be clearly due to the increase of the surface in this region during the earliest phase of anthropogenesis. The conditions of development in this area seem not yet to have acquired a definite stability. One observes on this part of the skin, a very intense struggle for predominance between the hair streams, and hence the conditions vary considerably. I cannot at all agree with the statement of Kidd: "that the hair slopes at an acute angle with the plane of the surface, and always in a definite direction *which is constant for each region.*" The hair streams on the human forehead behave so whimsically that it is impossible to designate a given condition as representing the normal state; at best a certain one appears to predominate. Now it is very remarkable, that in the literature on the subject, I could not find a description which agreed with the condition which I found to be the commonest.

The first somewhat concise description of the hair streams on man is given by Eschricht, according to whom the various directions of the hairs depend upon the distribution of the vascular system. This description was followed by Voigt's essay, in which the subject was treated more thoroughly. According to this author the hair slope is dependent on the course, which the enlargement of the body takes in early stages of development. The change from the perpendicular to the sloping direction of the hair germs is produced by the stretching of the skin. Though this author gives a very elaborate description, it is clear that his conception of the hair stream system is too schematic. The whole surface of the body is divided into a number of regions and within each region there is one whorl from which a stream radiates.

These diverging whorls are according to Voigt the essential elements of the hairy covering. Converging spirals, crosses, crests, boundary lines between adjacent regions, etc., are all secondary phenomena. The extent of the regions is very varied and the course of the boundary lines therefore very complicated.

So the structure of the whole system is reduced by Voigt to some few divergent whorls, viz. the occipital whorl, the bilateral facial whorl (near the median corner of the eye), ear whorl, armpit whorl and the groin whorl. It is undeniable that the above-mentioned spirals are characteristic features of the hairy covering of man, but it was an erroneous view Voigt took when he considered them as the essential features of this covering.

The incompleteness of the descriptions given by this author has already been pointed out by Schwalbe in his elaborate investigation on the hair stream system in Primates. This author also declares Voigt's standpoint to be incorrect and is more inclined to agree with the views expressed by Thompson<sup>1</sup>, who supposes that the directions of the hairs are determined by the necessity of offering the least possible resistance to the air, grass and other obstacles while the animal is in motion.

In one of his studies on the hair slope Kidd<sup>2</sup> asserts that the characters of the hair slope are due to certain habits and surroundings of animals and that thus they are the result of Lamarckian factors, for the sloping direction of the hairs is due to the constant slight pressure to which the hairs are subjected before birth, and even more so, in after-life.

The author has applied these ideas to the region which is the subject of the present paper, in the following way. "In the frontal region," he says, "a slope of hair is found which results from a coalescence of the streams belonging to the scalp and interorbital region. Over the frontal region the stream passes to each side in a curving direction to the temporal regions. Towards the orbits it is lost in the eyebrows, and towards the scalp it passes in a curve parallel to the median plane to the edge of the scalp. Towards the frontal eminences the direction has changed so as to point to the temporal region. The only peculiarity in this region is the direct opposition between the stream from the forehead to the scalp, and that from the scalp to the forehead."

After this description which, in general, is accurate, the author continues: "It would seem that the action through many generations of methods of dressing hair, afford the traction necessary to produce this peculiarity."

These quotations make it clear that the aetiological factors for the hair slope are considered by Kidd as being purely mechanical, viz. pressure and traction. Now the great variability in the hair slope on the human forehead is a sufficient indication that mechanical influences cannot be the real factors determining the directions of the hairs. There must be other factors more physiological in character.

<sup>1</sup> Art. "Anatomy of Animals." 1895.

<sup>2</sup> "Notes on the Hair slope in Man." *Journ. of Anat. and Physiol.* vol. xxxv, 1900.



A complete survey of this anatomical phenomenon can only be obtained by investigating a large number of human foetuses in a particular phase of development. Friedenthal's statement, that the investigation of the hair streams in man should preferably be carried out upon foetuses in the eighth month of development, is undoubtedly an inaccurate one. I have found that an exact determination of the hair slope in the frontal region of human foetuses is only possible in specimens of 12 to 20 centimetres from vertex to coccyx. In older specimens the hairs on the forehead have grown too long, and the sebaceous matter between them renders the determination of their real slope difficult and inaccurate. I examined sixty foetuses of the above-mentioned length and this large number enabled me to obtain a somewhat complete survey of the variability in this region.

Before communicating the results of my investigation I will give the following summary of Voigt's description of the hairy covering on the frontal region of the human foetus. The stream of the vertex whorl, which is turned forward, forming a median and two lateral frontal streams on the forehead, meets the ascending facial streams at the level of the eyebrows. At the point corresponding to the Foramen supraorbitale the latter streams, running in an opposite direction from the eyebrow, cross. Between both crosses the ascending internal eyebrow stream meets the descending median frontal stream, forming a convergent whorl on the median plane, between the eyebrows: the so-called frontal whorl. Thus the region between the eyebrows should be characterized by two crosses near the eyebrows and by the whorl.

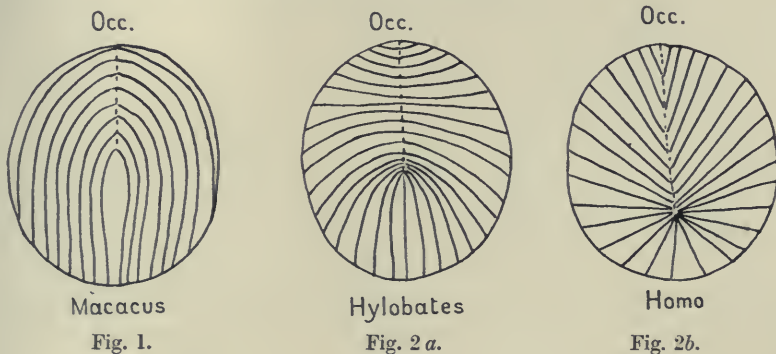
It is very remarkable that Voigt describes as normal a condition whose occurrence I doubted for some time, until at length I observed it in the foetus of a Javanese woman. This, however, was the only specimen out of the sixty I investigated which was in accordance with Voigt's description. Obviously the hair pattern is rarely so simple and symmetrical as this description suggests. It is curious that Voigt's attention has not been drawn to the fact that asymmetry is the rule and the symmetrical condition an exception.

It is necessary to lay stress upon this fact, because asymmetry, though the rule in the hair stream pattern of man, is absent in monkeys and even in apes. It seems, therefore, to be a typical human characteristic. Now as the direction of the hair streams in man is, in most cases, quite different from that in apes, a few remarks concerning the ape may be made.

A very elaborate investigation on the hair slope in apes has been carried out by Schwalbe who also makes some remarks with regard to the human system. These are of a provisional character, the author intending to deal with the results of his research on the human hair slope in a special publication. The realization of this intention, however, was prevented by his death. Yet, though Schwalbe's remarks are of a provisory nature, they are not without interest to us, as the author gives an hypothesis as to the manner in which the hair pattern on the calvarium of apes is transformed into that of man. This hypothesis is apparently founded on an insufficient number of observa-

tions, and it will become clear in the course of the present paper that Schwalbe's views are erroneous.

As a fundamental difference between man and ape, Schwalbe mentions the fact that on the forehead of man the hairs are directed forwards, in apes on the contrary, backwards. In general this remark is correct, but the author's opinion on the manner in which this change of direction was brought about is surely wrong. His view of the subject is illustrated by the following figures. Fig. 1, representing the scalp of *Macacus cymmolgus*, shows how in this monkey an ascending stream, which I will distinguish as the "facial stream," begins at the orbital ridges, the hairs on it having a backward direction. This stream is symmetrically divided by a parting extending from the root of the nose to the vertex. Now it is Schwalbe's opinion that, with regard to this parting, the hairs first turned in a more transverse direction (fig. 2a), as is actually the case in Siamang and after this turned forwards, while at the end of the parting, in the vertex, there arose a diverging whorl (fig. 2b).



This way of representing the transformation of the pithecoïd condition into that of man is certainly very simple, but observations made by the author himself should have aroused a strong doubt as to the correctness of his hypothesis. For among his descriptions there is one of a *Macacus*, in which a diverging whorl was present on the vertex, while the hairs were not turned forwards at all, but backwards in the normal way. In *Macacus* therefore, a vertex whorl can coincide with an ascending hair stream extending from the orbital ridges to the neck. Such a condition, in which the whorl is situated in the middle of an ascending stream, is not in accordance with Schwalbe's hypothesis.

I wish to lay special stress upon the above-mentioned observation of Schwalbe's because it demonstrates that the vertex whorl ought to be considered as a new element in the hair stream pattern of the head. If we take this fact into consideration it is easy to understand the fundamental plan of the hair pattern on the frontal region of man, and its more frequent variations.

In order to give a methodical description it is necessary to group the various conditions I have observed.

As already mentioned, the normal condition in apes is a symmetrical one, whereas in man such a condition is not the rule, as I found it in fifteen cases only; so that as a general rule the hair pattern on the human forehead is irregular. This, however, is a characteristic man acquired in the earliest phase of his evolution, and as the symmetrical condition is the original one, this must be the starting point of our exposition.

By way of introduction the hair pattern on the forehead and face of a young Gorilla has been drawn in fig. 3. Here the condition is still purely symmetrical. The forehead is covered by a left and right hair stream, diverging from a parting in the median line which extends from the root of the nose to the vertex.

In the lower part of the forehead, which in the foetus of Gorilla is markedly projecting, there is a horizontal hair slope, which gradually forms a more acute angle with the parting, the hairs taking a more sagittal direction, so that on the vertex and in the occipital region there is only one hair stream in which the hairs are directed parallel to the median line.



Fig. 3.



Fig. 4.

This condition, peculiar to the Gorilla and the other Anthropoids, I did not meet with in a human foetus excepting in two specimens where there was a hair pattern partly conformable to it; this appears to me to be the most primitive state occurring in man (see fig. 4). In these two foetuses there is a hair stream beginning in the interorbital region and covering the whole forehead and face. It is identical with the "facial stream" in apes. Its bilateral radiating point lies near the median corner of the eye. From this starting point a part of the stream bends downwards, covering the nose (nasal portion) and the cheek (buccal portion). The principal part of the facial stream however ascends and covers the whole forehead. As in the Gorilla, this stream is symmetrically divided by a parting into a left and a right half. The direction of the hairs is not straight but curved with a wide bend pointing to the temporal region.

Between the descending (nasal) part of the facial stream and the ascending



portion, a crest appears in the median line at the root of the nose which is one of the most constant formations in the human hair pattern. We will distinguish this as the "nasal crest."

In the upper part of the forehead the facial stream meets with a second stream, issuing from the vertex whorl, in which the hairs are turned forward. This will be called the "*bregmatic*" stream. In the specimen represented in fig. 4 it was symmetrical, but without parting, the hair slope being nearly parallel to the median line.

The boundary line between the facial and the bregmatic stream almost coincides with the frontal edge of the hairy covering of the scalp. In the middle of the line of convergence between both streams a second crest is formed which will in future be mentioned as the "frontal crest."

After the description of this most primitive state occurring in man a question may be put as to the relation between this condition and the one found in Gorilla. As already remarked Schwalbe's idea is very suggestive through its simplicity, but it is not in accord with the facts. I think the starting point for the comprehension of the human condition must be the fact observed and described by Schwalbe, that in *Macacus* there is a vertex whorl in the centre of a facial stream, extending from the eyebrows to the neck. This vertex whorl I consider as the beginning of the bregma stream in man, in whom it has considerably enlarged, as a result of the increasing surface of the head. Moreover this new element in the hair pattern has driven back the facial stream, so that the boundary line between both streams coincides with the anterior border of the hairy scalp.

Thus, the hair pattern on the human forehead and scalp may be regarded as the result of a struggle between a new element and a primitive one, the former being the stronger. The fact that this new stream originates in the median line of the head is perhaps an indication that the expansion of the skin of the head during human evolution took place along the median line.

That the idea of a struggle between two elements is not a metaphor but a reality is shown by a group of variations in which the hair pattern is also symmetrical, but in which the bregma stream gradually enlarges its territory across the forehead, driving back the facial stream. The successive phases of this process are demonstrated by the differences in topography of the frontal crest, and by the boundary line between both streams.

In fig. 5 the condition is drawn in which the bregma stream extends its territory down over the whole forehead, the frontal crest being now situated somewhat above the glabella. In this specimen the facial stream is pushed



Fig. 5.

back almost to its extreme limits. I have not met with a specimen in which the bregma stream invaded the region beneath the eyebrows. When the frontal crest is situated just between the eyebrows the boundary line between both streams passes through the eyebrows. This condition I found in one specimen only; both eyebrows showed a fine feathered structure, the upper hairs converging at an acute angle with the lower ones.

The successive enlargement of the territory of the bregma stream, with maintenance of the symmetrical condition, I found in twelve of the sixty foetuses I examined.

I have laid stress upon the fact that the bregma stream as a new element in the human hair pattern, started in the median line, for from this fact I conclude that the expansion of the scalp during man's evolution started from this line, and this conclusion is corroborated by the following phenomenon. In most cases the boundary line between the bregma and facial streams is not a straight line, but a curved one, as the median part of the



Fig. 6.

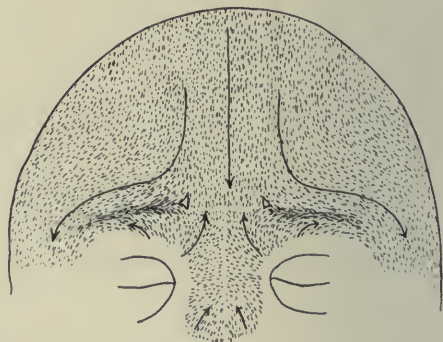


Fig. 7.

bregma stream is pushed farther forward than the lateral portions. Fig. 6 shows how the bregma stream penetrates, like a wedge, into the facial stream.

The next stage of development of the hair pattern in man's frontal region is represented in fig. 7. The condition sketched here is regarded by Voigt as the normal one in the human forehead. The inaccuracy of this view is sufficiently shown by the fact that I only observed this condition once, in the foetus of a Javanese woman. Up till then I was in doubt whether the condition described by Voigt was not hypothetical, arising from the author's endeavour to reduce the human hair pattern to the simplest form. The condition drawn in fig. 7 is of importance as a proof of the actual existence of the condition Voigt describes as being normal. Its chief significance, however, lies in the fact that it is the key to the comprehension of the remaining variations of the hair pattern on the human forehead which are all characterized by their asymmetry. The condition sketched in fig. 7 is still closely symmetrical, and resembles that in fig. 5. In both cases the bregma stream has extended to the



region between the eyebrows, thus forcing back the facial stream. But if attention is paid to the frontal crest, one will at once be struck by the difference between both conditions. For in the individual from which fig. 5 was drawn, this crest lies in the median line, and to the right and left of this the bregma and facial streams meet at a sharp angle. In the specimen shown in fig. 7, however, the median frontal crest is lacking, and instead of this one finds at the median end of each eyebrow a triangular formation; the diamond-shaped frontal crest has, as it were, been divided into two halves.

Between the two eyebrows ascending perpendicular lines of the facial stream meet the descending lines of the bregma stream, thus forming a line of junction running transversely and connecting both eyebrow triangles.

The lateral portions of the right and left bregma stream of the individual drawn in fig. 7 take a direction as in fig. 5, and in the outer side of the eyebrow triangles the hair lines of this stream strike the lateral portions of the facial stream at a sharp angle. In this way a line of convergence is formed running through the eyebrows and giving them a handsome, feathered appearance.

It is not difficult to deduce the condition sketched in fig. 7 from fig. 5. The first is more complicated because a new element has been added to the hair pattern, or, more rightly speaking, two new elements.

Firstly, the median portion of the bregma stream has developed into an independent element, which is characterized by the fact that the hair lines do not curve outwards but continue in a downward direction as far as the eyebrow level. In order to facilitate the description of the remaining types, I will distinguish this stream as the "upper intermediate stream."

A second complication has arisen through a differentiation of the facial stream. Here also the median portion has acquired a certain degree of independence, for while in fig. 5 all the hair lines in this stream are curved in a lateral direction, this is not the case in fig. 7. Between the eyes the hair lines of the right and left facial streams converge and form a median vertical line of convergence at the root of the nose; after this they bend straight upwards and form a transverse convergent line with the upper intermediate stream, only curving laterally in that portion of the facial stream situated between the upper eyelid and the eyebrows.

This median portion of the facial stream, which has thus become more or less independent, will in future be distinguished as the "lower intermediate stream."

The complication which has arisen in the hair stream pattern fits logically in the scheme of development we suggested when searching for the manner in which the simple symmetrical type of human hair stream might have developed from the lower Primates. For then we summed up the evidence for the supposition that the changes which led to the development of the human type took place in the median plane. It was in the median plane that the vertex whorl first appeared thus giving rise to the bregma stream; the conquest of the facial stream by the bregma stream is always pushed farthest



in the median line, and now it appears that the median portions of both streams can emancipate themselves from the mother stream and can form more or less independent streams.

The large number of specimens I examined has made it possible for me to follow the gradual transformation of the pithecoïd to the human condition. For among this large collection I found a sufficient number of symmetrical conditions (viz. 15 out of 60) to become thoroughly acquainted with the curious process of supersession, by which a primitive stream gradually loses ground in favour of a newly arisen stream.

With limited material this general insight could not have been obtained, as in most individuals asymmetrical hair patterns are found with great variety of structure, and, as we have remarked already, these can only be interpreted by a study of the complicated symmetrical type drawn in fig. 7.

The conditions hitherto described have surely sufficiently proved that Schwalbe's view of the manner in which the human frontal hair pattern was formed from the pithecoïd form, is entirely incorrect. A simple change of the hair slope in an existing stream, as supposed by this author, has never taken place. The original stream has been superseded by a new one, with a contrary slope.

I have thought a great deal about the possible cause of this process of supersession, this reversal of the hair slope, but without success.

One can, of course, think of the changes which the scalp would undergo as a result of the expansion of the skull. But then one must not lose sight of the fact that the scalp of Gorilla and Chimpanzee have considerably increased in surface in comparison with the lower Primates, while both these apes have retained a hair pattern such as is found in the latter creatures.

The solution of this problem becomes more difficult when we take into consideration the fact that the human forehead has never possessed a permanent hairy covering; here we have to do with processes which are limited to the temporary foetal hairy covering, at any rate for the greater part.

One could, moreover, consider the influence of the exceptional projection of the human forehead during the phase of development in which the foetal hairy covering develops. But the forehead of the Gorilla and Chimpanzee also projects considerably in that stage of development in which the frontal skin becomes covered with hairs. The transformations in the external shape of the head, under the influence of the very considerable development of the skull, do not seem to have been of any importance here, nor do external factors, for the frontal portion of the hairy covering only had but a temporary intrauterine existence.

And yet there must be causes which determine the hair pattern on the forehead in general, as also its variability; and one may say that this is brought about by directions of growth in the skin, but in this way one only shifts the difficulty, for the directions of growth must also be dependent on certain causes.

Finally, if one maintains that the structure of the frontal hair pattern is, in every case, only determined by casual circumstances, and as a proof of this assertion refers to the great variability, it is also evident that, if this is true, all variations must appear with equal frequency, at any rate in the asymmetrical conditions. This, however, is by no means the case. For in nearly the half of the individuals examined the same asymmetrical structure of the hair pattern appeared.

This structure, represented in fig. 8, was encountered in twenty-five of the sixty cases examined, albeit with individual modifications and, as already remarked, the total number of asymmetrical structures amounted to forty-five.

The system represented in this figure is very different from the symmetrical structures described heretofore. Both the chief streams, the bregma and facial, are recognizable, and the asymmetry is evident in the region of both.

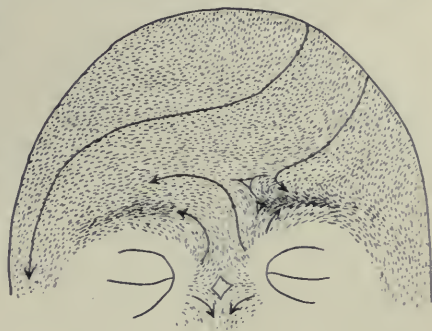


Fig. 8.

This asymmetry is caused by the fact that in the territory of the bregma stream as well as in that of the facial stream the boundary line between the right and left streams has been shifted to the left side of the forehead. In other words the hair lines or hair rows, *i.e.* the ascending facial stream as well as the descending bregma stream which run across the right half of the forehead, begin chiefly to the left of the median line. One can also describe the condition in the following way, viz. that a portion of the left bregma and facial stream have joined the right one, so that one gets the impression that the right half of both streams has widened out at the cost of the left half.

The result is that on the largest part of the forehead the hairs run more horizontally from left to right. Of the intermediate streams mentioned above, only the lower one is present and this curves entirely to the right side of the forehead.

One of the most striking consequences of the asymmetry in the hair pattern is the difference in structure of both eyebrows. The right eyebrow lies in the midst of regular hair lines running laterally; the result is a structure much resembling a paint brush. But the left eyebrow coincides with the line of convergence between the left facial and bregma streams, which gives it a more feather-like appearance.

To the median side of the left eyebrow lies the frontal crest, which in these cases is built up in a more or less evident manner out of two triangles, situated closely one above the other.

As already remarked this type of hair stream is found, with certain individual peculiarities, in nearly the half of all human beings. From this it

seems very natural that in most individuals the direction of the hairs along the anterior edge of the hairy scalp is from left to right, and that in consequence the wearing of a parting on the left side of the head is in accordance with the most frequently occurring direction of the hair growth.

The difference in structure of both eyebrows as a result of the asymmetry of the hair pattern is a phenomenon which one can still often detect in young individuals. At an older age, on the contrary, the difference disappears; the left eyebrow loses its feathery appearance and one gets the impression that both eyebrows are formed from the facial stream.

Only once did I come across a condition which was in every respect the mirror image of fig. 8. This was in a Malayan foetus.

In figs. 9 and 10 two conditions are depicted which can be regarded as variations of fig. 8. In fig. 9 the hair lines of the bregma stream run more perpendicularly, and it is only in the centre of the forehead that they bend to

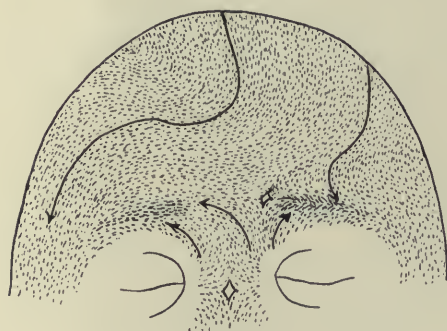


Fig. 9.

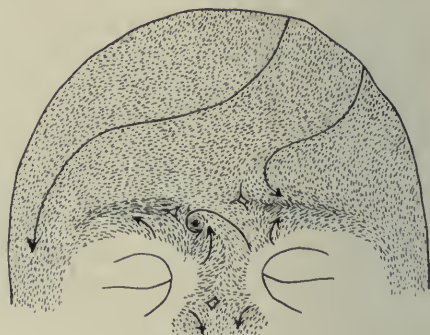


Fig. 10.

the right at a fairly sharp angle. In this manner loop-shaped hair lines are formed on the right-hand upper portion of the forehead. Otherwise the condition is the same as in fig. 8. In three cases I observed a similar pattern.

More interesting is the variation seen in fig. 10 as here a new element in the hair pattern is visible. The direction of the hairs on the forehead above the eyebrows entirely corresponds with fig. 8; we also see here the difference in structure of both eyebrows. The lower intermediate stream, however, behaves very curiously. While in normal conditions the hair lines coming from the left cross the median line and push themselves in between the left bregma and facial streams in the region above the right eyebrow, in fig. 10 they form a converging whorl with the hair lines coming from the right, the point of convergence lying slightly medial to, and under, the right eyebrow. This variety I also observed in three cases.

Higher up I already mentioned that I had only once observed the mirror image of the most prevalent condition, shown in fig. 8. A hair slope from right to left in the forehead can therefore be regarded as an exception. Twice, however, I came across a hair pattern in which this was partially the case.



These two, which can be regarded as rare cases, are drawn in figs. 11 and 12. Both have this in common, that the lower intermediate stream slopes from right to left, and above the left eyebrow joins the left bregma stream. In both cases the eyebrows have a brush-like structure.

This variety in the direction of the lower intermediate stream is accompanied by an extension of the left bregma stream across the right half of the forehead. In fig. 11 the hair lines in this stream slope straight downwards in a broad median band, only turning fairly sharply to the right and left just above the eyebrows. Some of the hair lines on the right half of the forehead, on the contrary, curve to the left, with the result that the frontal crest is situated at the median end of the right eyebrow.

In fig. 12 the bregma stream shows the same type, except that the hair pattern is not so regular here, as the hairs are directed from left to right in the upper portion of the forehead. It is only in the region of the glabella that

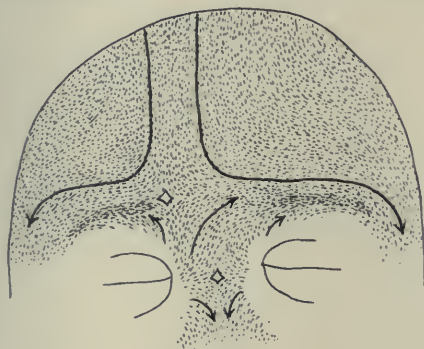


Fig. 11.

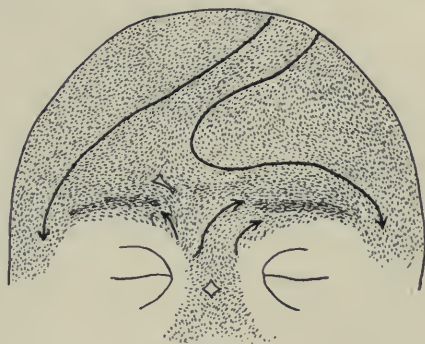


Fig. 12.

the left bregma stream crosses the median line, bending sharply to the left afterwards. Here also the frontal crest lies in the immediate neighbourhood of the right eyebrow.

We can now proceed to the description of a group of variations which differ from those hitherto mentioned in the great irregularity of the hair pattern.

The variations belonging to this group have one characteristic in common, viz. that in the hair pattern of the forehead a whorl has been formed, which I shall distinguish as the frontal whorl. This, however, is the only thing they have alike, for the presence of this whorl is accompanied by such excessive irregularity in the further structure of the hair pattern that I have not met with two individuals possessing the frontal whorl who had any other similarity of their hair pattern. This is evident from figs. 13 to 17, where five cases are depicted which possessed a frontal whorl. The great variability of the hair pattern in individuals with such a whorl is shown by the variation in both shape and situation of the whorl.

The character of the whorl differs, for at one time one sees it converging,

that is to say, the hair lines run in a spiral slope towards the central point of the whorl, then again it diverges, the hairs sloping away from the central point, just as is the case in the vertex whorl.

The situation of the whorl also differs, being now higher, now lower, but always (at least in the cases I observed) on the upper half of the forehead; moreover it can be found either in, or at the side of, the median line, and either to the right or to the left.

This difference in character and situation of the whorl is the cause of the great variability of the hair pattern in this group, and I am convinced that, on further investigation, patterns of the hairy covering of the forehead, other than those drawn in figs. 13-17, will be discovered. The conceivable possibilities are numerous.

The hair pattern of the forehead acquires a certain elegance when a whorl is present owing to its complicated structure. If one considers that among



Fig. 13.

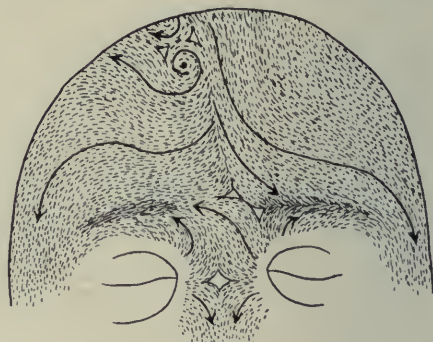


Fig. 14.

sixty individuals a frontal whorl was observed five times, then its appearance need not be regarded as a rarity.

Is the occurrence of this whorl to be considered as a progressive phenomenon in the development of the hair stream system on the human forehead? I am inclined to answer this question in the affirmative, on the following grounds.

I have said previously that the appearance of the vertex whorl in the region of the occiput should be regarded as the beginning of the development of the human hair pattern.

This vertex whorl arose in, or near, the median line in the middle of the facial stream, which originally ran on to the nuchal region. The transformation of the pithecoïd hair pattern to the human one began therefore in the median line. Subsequently I drew attention to the fact that the supplanting of the facial by the bregma stream had always gone farther in the median line than laterally (cf. fig. 6). The differentiation of the human condition from the pithecoïd appears, therefore, to have started in the median line.

This opinion is further proved by the situation of the frontal whorl, for



this also appears in the median zone of the forehead, sometimes, as in fig. 13, just in the median line. The appearance of the frontal whorl gives the impression of being a repetition of the process which led to the formation of the vertex whorl.

This most interesting complication in the hair pattern of the human forehead is a new proof in favour of the assertion that the hair slope is not determined by external causes, but is dependent on internal factors, for it appears in the foetal hair pattern of the human forehead. Before birth this hair has already been cast off, and this part of the hairy covering has, therefore, never been subjected to external factors. So its structure and progressive development cannot have been the result of influences working from without.

It is of small importance to describe separately the different cases given in figs. 13-17; the drawings are, I believe, clear and complete enough to give a correct impression of these very complicated and at the same time variable conditions.



Fig. 15.

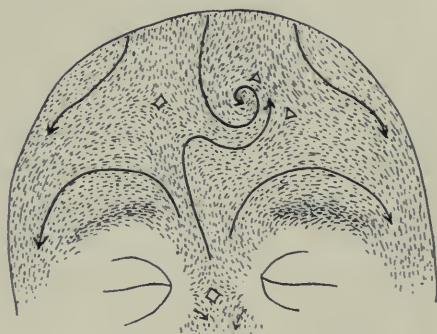


Fig. 16.

Only to one case should special attention be drawn, viz. fig. 17. For here one sees the very rare appearance of two whorls instead of one: a diverging frontal and a likewise diverging eyebrow whorl, both slightly to the right of the median line.

We have already seen an eyebrow whorl in a previous case which is depicted in fig. 10. The existence of two whorls, however, on the forehead must certainly be regarded as a curiosity.

If one compares the eyebrow whorl of fig. 17 with fig. 10, then one sees a remarkable difference. For though in both individuals its position is identical, it is a converging whorl in one case (fig. 10) and diverging in the other (fig. 17). This fact tends further to obscure the factors which determine the hair slope. For if in one case it is towards a certain point on the surface of the body and in another case turned away from it, it is evident that this point certainly has significance with regard to the hairy covering, and that the implantation of the hairs in relation to this point is dependent on varying factors.

It has already been remarked that this last fact also holds good with



respect to the frontal whorl; in figs. 13, 14 and 17 it is divergent, in figs. 15 and 16 convergent. An accurate comparison of the structure of the hair pattern in both groups, however, teaches us something in this case about the possible cause of the difference.

In the foetuses sketched in figs. 15 and 16 the ascending facial stream extended across a fairly considerable area of the forehead, while in the three other cases (figs. 13, 14 and 17) this stream had on the left side been pushed back as far as the eyebrow by the descending bregma stream. It is possible that this is a coincidence but it is also possible that the character of the whorl has been determined by the struggle for territory, which is constantly being waged between the bregma and facial streams. The result would then be as follows: if the ascending stream is predominant a convergent spiral is formed, if the descending stream gets the upper hand a divergent whorl appears.

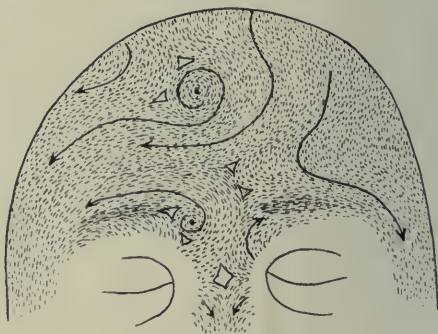


Fig. 17.

The study of the hair streams on the human forehead does not lead to the results one would have expected. The variability in the structure of the hair pattern is so great in this region of the skin that one scarcely comes across two individuals who are entirely the image one of the other. Now one would expect that a study of this excessive variability would lead to a solution of the causes determining the hair slope, but this is in no wise the case.

The only conclusion which could perhaps with some justice be drawn from a comparison of the different conditions, is that the hair slope is not determined by external influences but that it is probably the expression of certain conditions of growth in the skin. We are still, however, entirely in the dark as to the actual connection between the process of skin-growth and the hair slope.

I will conclude this short essay with a remark about the great variability of the hair pattern on the human forehead.

The material employed for this investigation consisted of foetuses chiefly from Dutch mothers, only eight being derived from the population of Java. Now the Dutch population must anthropologically be considered as a very mixed one, many races having contributed to its formation. This fact raises the question whether this great variability in the hair pattern could not be a result of the excessive mixing of races out of which the present population of Holland has been formed. Would such a variability also be found in individuals of a purer race or would not each race be characterized by a frontal pattern of its own? This question seems to me, from an anthropological point

of view, to be well worth considering, and an investigation in this direction would be of value.

In such an investigation the question of the heredity of the hair pattern would stand uppermost. This last question is certainly not an easy one to answer with regard to such a very mixed population as exists in civilized states. Moreover one cannot reconstruct the foetal hair pattern after birth when the lanugo has been cast off, so that an examination of children of the same parents also gives no result.

There is, however, another way of answering this question, viz. the comparison of the hair pattern of dicephalic double-monsters, which are in the fitting stage of development for this investigation. I had the good fortune to be able to examine the structure of the hair pattern of two dicephalic monsters. The result was rather surprising, for while on both heads of one dicephalus I found an entirely identical hair pattern, there were considerable differences in the two heads of the second monster. They certainly both belonged to the asymmetrical type sketched in fig. 8, but they differed very markedly in detail.

## MECHANICAL CONSIDERATIONS IN THE SCAPULO-HUMERAL ARTICULATION

BY GORDON HARROWER, M.B.

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THAT the shoulder-joint should be so lax anatomically may not occasion surprise when one considers the great range of movement permitted; that such a combination is capable of lifting heavy weights from the ground, not to mention raising the weight of the body as in climbing, is indeed remarkable.

Suppose we consider the feat which one commonly sees performed by athletes, that of lifting a 56 lb. weight from the ground into the position of complete abduction, i.e. making an angle of  $91^{\circ}$  with the sagittal plane. The elbow joint being in complete extension the ulna and humerus together constitute a lever of the third class, that is, the weight to be lifted is at one end of the lever, the fulcrum at the opposite extremity and the force applied somewhere between these two points. As is generally recognised this is one of the least efficient mechanical forms of lever, its advantage being that it permits great range of movement.

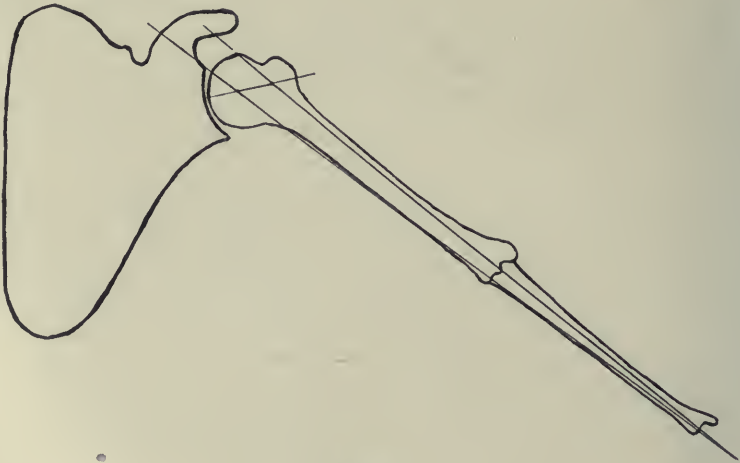


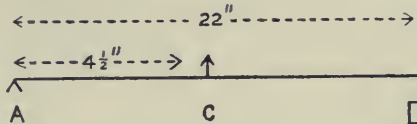
Fig. 1.

The axis of the effective lever does not correspond to the axis of the bony members on account of the obliquity of the anatomical neck to the shaft of the humerus. The true axis of the lever therefore is distinctly below the axis of the bones so that a triangle is formed in which the base is the axis of rotation, while one side is formed by the axis of the bones and the other by the axis of the neck and head of the humerus. This fact is of considerable importance in two ways: (1) the mechanical strength of the lever is increased, (2) rotation round the axis is permitted and this necessitates some method of preventing



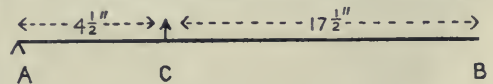
internal and external rotation thus requiring a further expenditure of power, a straight lever being more easily controlled than a bent one. Rotation, or as Fick prefers to call it, pronation and supination, is prevented during abduction by the attachment of the muscles to the tuberosities. The subscapularis checks external rotation, while the teres minor and infraspinatus check internal rotation, the anterior and posterior fibres of the deltoid also acting. A marked feature in lifting heavy weights under the conditions mentioned, is the bracing of the shoulder; the muscles attaching the scapula and clavicle to the axial skeleton are strongly contracted, the internal rotators acting more powerfully to counteract the distinct tendency to external rotation. The supraspinatus has little or no effect on rotation. We are now in a position to consider the fixation of the head or fulcrum.

Taking the length from the fulcrum to the centre of the palm of the hand as 22 ins. and the distance from the fulcrum to the insertion of the deltoid as  $4\frac{1}{2}$  ins. and the weight to be raised as 56 lbs. by the following formula we find:



$$\begin{aligned} AB \times 56 &= AC \times x \\ \therefore 22 \times 56 &= 4\frac{1}{2} x \\ \therefore x &= 274 \text{ lbs. approx.} \end{aligned}$$

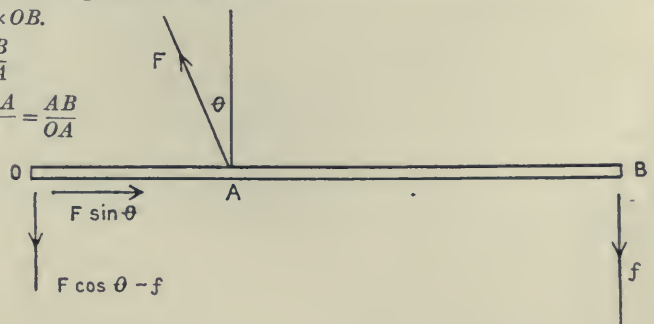
In raising the weight from the ground to a point at right angles to the body, the muscles involved (directly as abductors as opposed to muscles fixing the fulcrum) are the supraspinatus and biceps applying force at a very short distance from the fulcrum. The latter muscle acts from its insertion to the origin of its long tendon into the upper margin of the glenoid ring and scapula. The deltoid is the chief effector both as regards the bulk of the muscle and its mechanical advantage of applying the force nearer to the weight to be lifted. The force at the fulcrum is proportionately equal to, and opposite from, the weight lifted. In other words at any instant during which the weight is being neither lifted nor lowered the system is in equilibrium<sup>1</sup>. There must therefore be a force acting on the fulcrum (i.e. the head of the bone) preventing its downward or upward displacement as follows:



$$\begin{aligned} 56 \times CB &= AC \times x \\ \therefore 56 \times 17\frac{1}{2} &= 4\frac{1}{2} x \\ \therefore x &= 218 \text{ lbs.} \end{aligned}$$

<sup>1</sup> Rod pivoted at  $O$ ; forces  $F$  and  $f$  applied at  $A$  and  $B$  as shown. Since the rod is in equilibrium the pivot must apply to the rod a horizontal force  $F \sin \theta$  and a downward force  $F \cos \theta - f$ . These forces are applied by the pivot to the rod; the rod applies to the pivot equal and opposite forces. Further, since the rod is in equilibrium, we have

$$\begin{aligned} F \cos \theta \times OA &= f \times OB, \\ \frac{F \cos \theta}{f} &= \frac{OB}{OA} \\ \frac{F \cos \theta - f}{f} &= \frac{OB - OA}{OA} = \frac{AB}{OA} \end{aligned}$$



that is, there is a force tending to displace the head of the humerus upwards or downwards equivalent to a weight of 218 lbs. I have chosen the period of equilibrium because in motion the muscle force is slightly greater or less according to whether the weight is being raised or lowered. On account of the force of gravity there is no normal tendency to a sudden upward displacement of the distal extremity and a consequent rapid downward displacement of the head, a fact which offers a further explanation of the lack of museular support of the head inferiorly, in addition to inheritance from a pronograde ancestry in which the weight of the body is partially supported on the humeri.

The head of the humerus is somewhat less than half a sphere and does not fit the glenoid cavity accurately. It has therefore no bony support such as is provided in the hip joint. The capsule is decidedly lax and affords practically no support to the head and there are no muscles acting directly to hold the head in place except in the horizontal position of the arm when the head receives some support from the long tendon of the triceps. The supraspinatus and biceps both use the head as a pulley over which to act and these two muscles therefore tend to depress the head until the arm has reached the horizontal position. We must therefore consider what other conditions assist in fixing the fulcrum.

If one wishes to move the arm freely as in rapid circumduction, the muscles producing the movement act in succession. The muscles which are not in immediate action although in a tonic condition are nevertheless comparatively lax, the centrifugal force tending to pull the head of the humerus away from the glenoid cavity thus allowing free lubrication. In heavy weight lifting, however, every muscle of the shoulder region is in powerful contraction, pulling the head against the articular cartilage of the glenoid cavity. This forcible compression of the articular surfaces squeezes the synovial fluid from the surfaces in apposition while at the same time flattening the surfaces and therefore increasing the friction between the two surfaces. Friction, however, is independent of the extent of the area in contact between two given masses.

The muscles acting to pull the head of the humerus against the glenoid cavity are the pectoralis major, latissimus dorsi, supraspinatus, infraspinatus, teres minor, subscapularis, biceps and deltoid.

*In toto*, the resultant of the various forces acting on the head of the humerus to fix the fulcrum is at right angles to the surface of contact in the glenoid cavity because the muscles automatically adjust the degree of their individual contraction to produce this, the most favourable condition. Assuming the curvature of the lower part of the glenoid cavity as being practically a plane surface (and this may be conceded considering that it is a segment of the circumference of a circle of relatively large diameter) then with the scapula fixed and having its vertebral border approximately vertical, this glenoid surface makes an angle of about  $67\frac{1}{2}^{\circ}$  with the normal horizontal plane (fig. 2).

The co-efficient of static friction which is always less than unity equals  $F/M$ , where  $F$  = muscular pull and  $M$  = the weight 218 lbs. tending to displace the head of the humerus.

In order that the mass may be raised the muscular force pulling the head inwards must be relaxed to allow the head to roll round in a downward direction in the glenoid cavity, that is, we must establish kinetic friction and as the weight is raised gradually, the movement inside the joint will tend to be

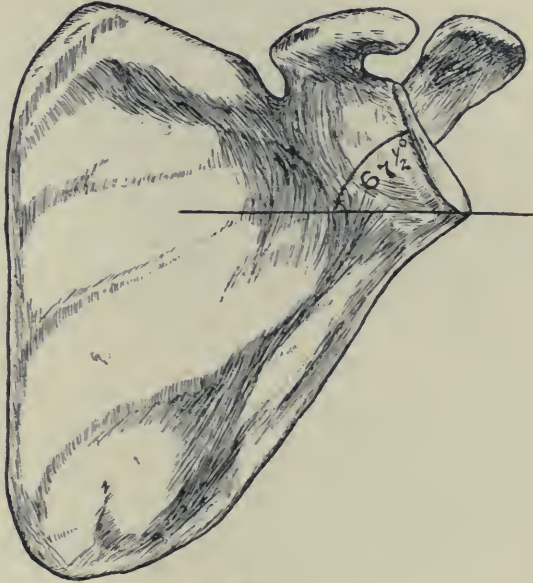


Fig. 2.

intermittent in type, on account of the much smaller range of movement at the joint compared to that of the hand. There is therefore, at various times an instant, just as static friction is about to become kinetic friction, during which a condition of balance is produced, when the angle of the surface of the glenoid cavity becomes the angle of repose or limiting angle (fig. 3).

The coefficient of kinetic friction =  $\tan \theta = F/M$ .

Since  $u$  (coefficient of static friction) =  $F/M$  and  $\tan \theta = F/M$

$$\therefore u = \tan \theta = \tan 67\frac{1}{2}^{\circ}.$$

We can now calculate the force acting on the head as  $F = M \tan \theta$ , which equals the minimum pull of the resultants of the various muscles acting on the shoulder joint to fix the fulcrum when a weight is being raised from the ground into a position of abduction

$$F = \frac{(W + C) \times CB}{AC} \tan \theta$$

where  $W$  = weight raised;  $C$  = weight of the arm;  $CB$  = distance from insertion of deltoid to hand;  $AC$  = distance from fulcrum to insertion of deltoid; and  $F$  = muscular pull on head of humerus.

We also note that in order to decrease the limiting angle the inferior angle of the scapula is rotated outwards at the commencement of the movement



and after the shoulder joint is completely abducted any further movement in this direction is always accompanied by flexion of the body to the opposite side, all in order to reduce the limiting angle. It may be noted that when the

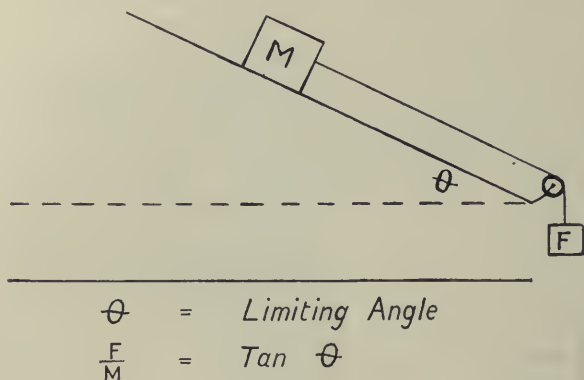


Fig. 3.

arm is adducted and in apposition to the lateral aspect of the body the limb is merely suspended by the muscles, assisted by the obliquity of the glenoid cavity with the humerus "hooking" on it.

Having considered the fixation of the head of the humerus and noted the strains involved we shall now consider the effect of such strains and stresses on the internal structure of the head of the humerus. In a section through the head of the adult humerus cut in the plane of the great tuberosity, an inverted V-shaped osseous lamina is noted. One limb of the V passes from the distal extremity of the great tuberosity upwards and inwards toward the head, meeting the other limb of the V which passes downwards and inwards toward the centre of the articular surface (fig. 4). This is apparently the modified epiphyseal line ossified and thickened. Cope has noted the persistence of the

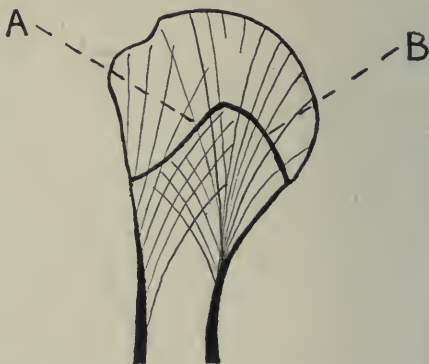


Fig. 4 (after Wagstaff). A. Pressure line due to pressure on the head of the bone. B. Tension line due to muscles attached to greater tuberosity.

line in patients over 60 years of age and states that the lines are prominent also in the head of the femur. I have sectioned both femur and humerus in a subject of 76 years of age and in both cases the line was very prominent, although better marked in the humerus. I have also found a small osseous lamina about one inch in length, placed vertically to the long axis of the shaft of the humerus in the region of the small tuberosity. This spur was present more or less in all the humeri I have sectioned and corresponds somewhat to

the calcar femorale but very much less developed. The persistence of the osseous laminae in the femur and humerus in the position of the epiphyseal lines, long after all trace of the epiphyseal line has disappeared in other situations is due to the enormous strains to which these bones are subjected.

In Morris's *Anatomy* the pressure curves in the head of the humerus are shown. One set at right angles to the greater tuberosity are correctly described as the result of tension exerted by the muscles attached to the great tuberosity. The other set at right angles to the articular surface of the head are left unexplained but are developed to prevent flattening of the head of the bone during the great pressure introduced in powerful abduction which I have indicated.

To my knowledge no one has indicated the mechanical reason of the direction of the epiphyseal plates. It is highly probable that their direction is due to the strains involved for even *in utero* muscular tissue as soon as formed is continually in action. To this fact has been attributed the constancy in appearance of the centres of ossification.

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## SOME POINTS IN THE MECHANISM OF THE HUMAN HAND

By T. S. KIRK, B.A., M.B.

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DURING the war I became associated with Mr Pringle, an engineer, in the making of an artificial hand. Our aim was to produce an efficient hand, that is, one with which real productive work could be done. In our first experiments we did not try to copy the human hand, not having realised its mechanical perfection; we copied instead that all-round useful tool, a pair of gas-pliers. This gives a grip like that between the tips of the thumb and fore-finger. We varied the width of the blades or fingers, and then added a second finger, as it were, on one side; this increased the "bearing surface" and was found to be a great advantage. After many experiments, however, we were forced to admit that we had failed; we had been unable to construct a universal tool-holder. We decided, therefore, to try to copy the human hand, the most perfect gripping instrument and the widest in the range of its adjustment, being equally adapted for delicate finger-tip grip and complete palm grasp. While making this model and while dissecting the human hand to ascertain how Nature had met the mechanical problems, there seemed to me to be certain aspects of the mechanism of the hand which it would be worthy to record.

We found, for example, in our model, that fingers springing from a rigid metacarpus would not give a proper palm grasp and we were unable to get an efficient grasp until we commenced our fingers close to the wrist. In order to obtain such a grasp we had to construct our artificial hand so that the parts representing the fingers and the metacarpal bones acted together, the former flexing and the latter extending simultaneously. In describing a finger as a mechanical unit, therefore, the corresponding metacarpal bone should be included in the unit with the phalanges; and the meaning of the synergic action of the flexors of the fingers and the extensors of the wrist seems to be more easily understood.

Then, again, on account of the obliquity of the flexor tendons in passing from the wrist to the fingers and the palmar concavity of the metacarpus, we found that in closing the hand the marginal fingers were drawn to the middle line as well as flexed. To overcome this we had to insert a narrow piece of metal transversely at the place in the hand which corresponds to the heads or the necks of the metacarpal bones. In the human hand this tendency to adduction is prevented, I believe, by the action of the strong dorsal interossei muscles.



We found also that in order to get a proper palm grasp it was necessary to have soft adaptable pads in the palm; otherwise an object grasped in the palm slipped about in the hand. We experimented with many materials and finally used sponge-rubber, as being in its physical properties more like the palmar pads of fat than anything else we could discover. At first our arrangement of these pads was somewhat haphazard, but after the pads in the human hand had been dissected to study their disposition we placed the rubber pads in a similar way and were rewarded with excellent results.

The palmar pads in the human hand have a very definite arrangement, but while there is an extensive description of their homologies with those of the foot, of their greater thickness in the European than in the Asiatic hand



Fig. 1.

and their smallness in the hand of the anthropoid, I have not found in any description a reference to them as an essential part of the structure of the hand as a grasping mechanism. I have appended, therefore, the following short description of what I believe to be the manner in which they are used.

There are three main pads, namely, the thenar, the hypothenar, and the metacarpo-phalangeal pad, and sometimes there is a small fourth one between the proximal ends of the thenar and hypothenar pads. The thenar pad overlies, but does not quite cover, the thenar muscles, their basal and lateral parts being bare. It is closely connected to the skin by a large number of fibrous septa, which require to be divided in removing the skin from it. There is a "tail process" from it which proceeds forwards and curves laterally under the web of the thumb. The hypothenar pad is larger and of greater thickness

than the thenar pad. It covers the hypothenar muscles and reaches at least the ulnar border of the hand, while underlying it and inserted into it from its deep surface there is the palmaris brevis muscle. Deep to this muscle there is a varying amount of fatty-areolar tissue, but in texture this is quite different from the pad, being soft and lobulated. The hypothenar pad has very little skin connection, the lines in this area of the palmar skin being remarkably few compared with those on other parts. The metacarpo-phalangeal pad lies across the roots of the fingers. It is divided into three parts. The central of these is common to the interval between the middle and ring fingers and to the adjacent parts of their bases, while the marginal pads are related to the index and little fingers and to the spaces between them and the central fingers and the adjoining parts of their bases. The intervals between these pads are indicated on the skin by flexure lines and the pads themselves are attached to the skin and underlying tissues.

When an object is taken in the hand and grasped with the palm these pads are applied and adapted to it so that the hand and the object become accurately fitted together. The pads, of course, will tend to be displaced. The thenar and the metacarpo-phalangeal pads, however, are retained in position partly by their skin connection and partly by the backing they have of the underlying muscles and bones; but the hypothenar pad, which would tend to be splayed round the ulnar margin of the hand, is held in position by the contraction of the palmaris brevis muscle. This then I put forward to be the purpose of this muscle, that it is a muscle concerned in the palmar grasp in which its action is to prevent the displacement of the hypothenar pad. In our artificial hand we had to support this pad by a strip of leather on the ulnar side in order to get its full benefit.

The points I wish to draw attention to are:

1. Considered as a mechanical unit the finger consists of the phalanges and the metacarpal bone.

2. In closing the fist there are required strong flexion of the fingers and moderate extension of the metacarpal bones: hence the attachment of the extensors of the wrist to the bases of the metacarpal bones, and the synergic action of the extensors and the flexors.

3. The pull of the flexors on the fingers towards the middle line is counteracted by the strong dorsal interossei.

4. The palmar pads are essential mechanical requirements for palm grasp: the ulnar one is the largest and the most useful, and, unlike the others, is free to be displaced; it is held in position by the palmaris brevis muscle.

# THE THICKNESS OF THE SCALP

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## INTRODUCTION

A KNOWLEDGE of the thickness of the soft tissues of the scalp has often been sought because of its obvious importance in the computation of head measurements on the living from those of the dried skull or *vice versa*. No satisfactory agreement has been reached for the simple reason that great variation occurs in the thickness of these tissues and determinations have been complicated by the condition of the post-mortem or cadaveric material upon which estimates have been calculated.

The methods adopted have been two: first, direct measurement by penetration of a needle (Welcker (16), His (6), Kollmann und Büchly (8), Czekanowski (4)), and secondly, by subtraction of the measurements upon the-fresh skull from those on the cadaver (Gladstone (5), Anderson (1)). Probably the latter method is the more reliable, especially for averages. The limitations of each method will be discussed later in this article. Although the subtraction method does not involve the error induced by deformation of the skin which can scarcely be avoided in direct determination, it is subject to instrumental error. This is especially true in the measurement of auricular height. Further on we shall show that it is essential to use an instrument of precision in making this observation.

Two other methods have been proposed but we cannot find that they have come into any general use. Nearly thirty years ago Welcker suggested radiographing the living head and measuring the thickness of soft parts directly upon the radiograms (17). He presented rather scanty data to indicate that the results of this method are quite comparable with those obtained upon



cadavera. Later on we shall show reasons for believing that the soft tissues of the scalp are not quite the same in the dead as in the living and this alone makes us somewhat dubious of the value of measuring shadows until radiographic methods have been more accurately worked out. The other method is that adopted by Pearson in the superposition of cranial contours upon those of skulls (2). This involves the use of different individuals, perhaps belonging to quite different social grades, and was only employed in temporary default of a better mode of attack.

We have undertaken to revise the existing data upon this important problem because we feel the imperative need of conducting, upon a specific material, a complete investigation of the various features necessary for a survey of the relation between measurements upon the head and upon the skull. Although the variabilities and correlations may not differ significantly from sample to sample the means undoubtedly do vary. One may not safely compare the means obtained from a sample of heads belonging to a particular social grade with the averages of a sample of skulls drawn from another. Hitherto there has been no serious attempt to determine all the necessary data upon a single population sample. We admit that there are objections to any group which may be chosen and the population of a dissecting room is no exception. We have reason, however, to believe that there are no greater objections to a population thus selected than to any other, and this group has the apparent advantage that it can readily be worked out completely.

In previous communications the senior author has set forth the necessary reductions for skull measurements upon the Reserve material (13) and has also presented data upon shrinkage of the cranium in drying (15), a source of error which must be considered. It is true, as Czekanowski has stated (4), that the alterations due to shrinkage do not result in an individual error greater than the probable average error in any calculated determination of cranial capacity, but we cannot hold with him that the effect of shrinkage can therefore be ignored. Having then these preliminary data to hand it is plain that what we still need for a complete set of observations rendering possible the prediction of cranial diameters from the comparable diametral measurements upon the living are: first, a consideration of the thickness of the soft tissues of the scalp and, secondly, a determination of the relation between these diametral measurements taken upon the living and upon the dead. Neither problem is simple but the latter is infinitely the more difficult.

All the observations necessary for this research have been determined by the senior author in the course of our routine examination of the cadavera and skulls in the Reserve collection. The data have been collected and reduced by the junior author and checked by the senior, who is also responsible for the form of presentation of this joint communication and for all the deductions drawn.

By the method adopted in this work the personal error remains constant throughout the entire series of investigations upon cadavera and skulls and

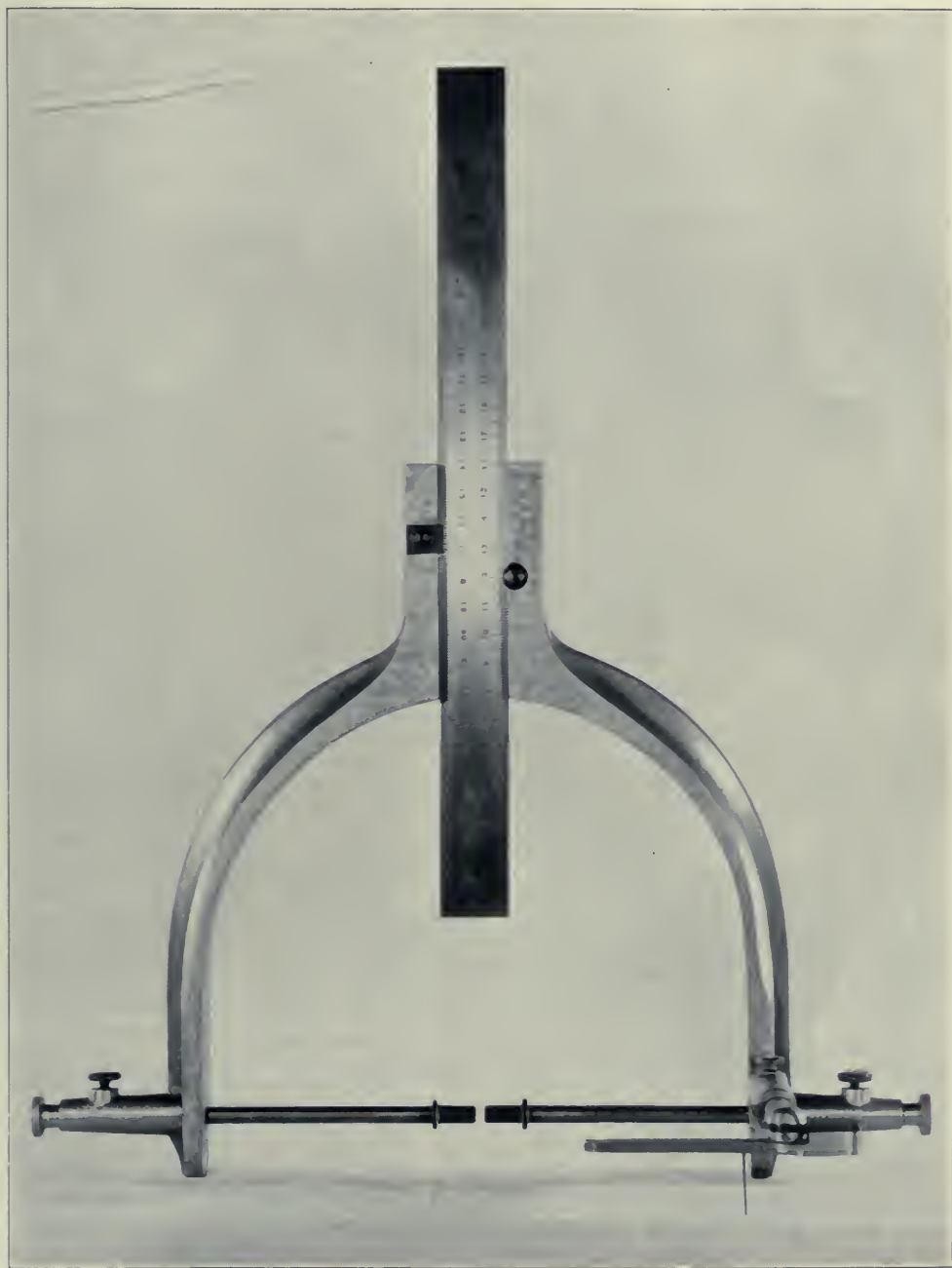


Fig. 1. The Reserve Head-spanner from the front. The ear rods are fibre tipped; the shoulders prevent the rods from penetrating too far into the ear passages. The infra-orbital gauge permits an accurate adjustment of the instrument in the Frankfort plane.

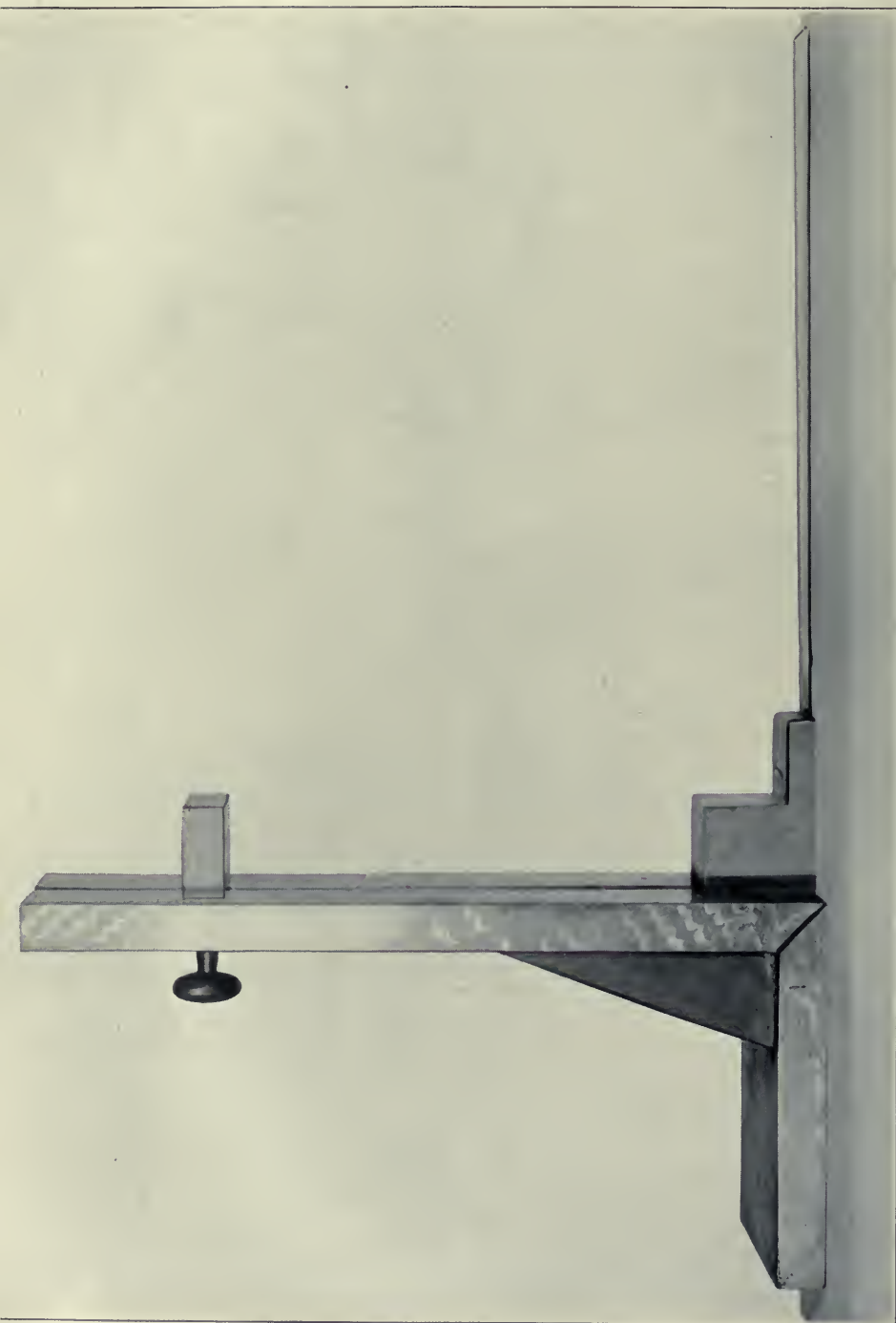


Fig. 2. The recently modified forward Cambridge Block used with the Reserve Craniostat.

A figure of the craniostat was published in this Journal, 1923, vol. LVII, p. 339. The base scale does away with the necessity of using millimetre paper. Zero on the scale is precisely under the free face of the upper measuring block. The craniostat and the hinder Cambridge block are slotted to permit the free passage of the scale. Length is read off on the scale at the point where it is covered by the free face of the hinder Cambridge block.



may therefore, for practical reasons, be discounted. For the most part the instrumental errors are known and have already been set forth. It is necessary, however, to discuss the error for an instrument which has not yet been described, namely the Reserve head-spanner.

#### THE RESERVE HEAD-SPANNER

The Reserve head-spanner, a modification of Gray's apparatus, is an all-metal instrument the principle of which is measurement of auricular height from the roof of the external auditory passage at right angles to the Frankfort plane. The instrument is illustrated in fig. 1. Zero on the scale is shown when the lower end of the scale is in contact with the upper aspect of the ear rods. The frame of the instrument is aluminium, the scale and rods are of steel, the tongue of the Frankfort gauge is of brass, and the rod tips of fibre. At first we made the rod tips of steel but these proved very uncomfortable in the ear passages. We next tried rod tips made from tooth brush handles but these were too brittle. The fibre tips can scarcely be called pleasant in the ear but they are the least objectionable. It is essential that the tips penetrate the ear passages sufficiently to rest against the roof of the bony canal; otherwise there is a large individual error. They cause actual distress if they penetrate too deeply. Consequently we constructed a shoulder 13 mm. from the extreme end. In using the instrument the tips should penetrate the canals sufficiently to rest in contact with the bony roof; they should not be pushed further in. The precise distance must be ascertained for each individual; the shoulder itself is not a sufficient guide. It is quite important to adjust the instrument correctly in the ear passages for the principle of our craniostat also is measurement from the roof just within the bony meatus.

The tongue of the Frankfort gauge was first made entirely of aluminium, but this metal proved too brittle. The antero-posterior rod is flattened on one side to prevent rotation and is held in position by a screw. The transverse limb moves freely in a horizontal direction by a joint permitting no vertical wobble. It is long enough for all practical purposes: if made too long it becomes inconvenient for use on narrow-faced individuals.

Once the ear rods are in position they are held securely in their bearings on the frame by the screws. The Frankfort gauge is adjusted to the lower border of the left orbit. The scale is then settled down upon the vertex and the auricular height read off directly. This instrument, like all others designed and made in the Anatomical Laboratory of Western Reserve University, may be purchased at cost on application.

#### RELATIVE ACCURACY OF INSTRUMENTS

The instrumental error for Flower's craniometer has previously been calculated (13) so that there is no necessity to engage in a new discussion of this instrument. For the measurement on hard surfaces the average error has been shown to amount to about 0.3 mm. either for length or breadth (13, p. 156) but in the former dimension there is a further source of error in the difficulty

of orienting the head of the cadaver exactly in the Frankfort plane. This difficulty adds about 0.2 mm. to the average error in length (13, p. 156). Assuming then that it is possible to measure the dimensions as accurately upon the soft tissues of the head as upon the hard skull, an assumption perhaps scarcely justifiable but yet necessary in the circumstances, we must admit that the average dimensions in the cadaver will not be more accurate than to 0.3 mm. for breadth and 0.5 mm. for length. The error in individual cases may be five or six times that amount.

In measurement of auricular height the standard of accuracy is the dimension as ascertained on the Reserve craniostat, the average error for which instrument amounts to 0.2 mm. (13, p. 156). When first employed, our craniostat had rounded rods for the ear passages but later we gave a knife-edge to those parts of the rods entering the external auditory meatus because the constricted orifice of certain skulls failed to permit the rounded rod quite to reach the roof of the passage. For a head-spanner to be employed upon the living it is not practicable to use knife-edges and therefore the Reserve head-spanner, as designed and made by our Mr Cherney, possesses ear rods with rounded fibre ends and in addition a shoulder the object of which is to prevent the rod from penetrating too deeply into the auditory passage. In those infrequent cases in which the upper part of the meatus suddenly narrows it has not yet been ascertained whether, on the living, the knife-edge would give a smaller measurement than the rounded rod. The cases cannot be diagnosed clinically. The difference rarely amounts to more than 0.25 mm. which is within the limit of personal error. It follows therefore that any difference between the two instruments in measurement of auricular height should result in the larger figure being derived from the head-spanner.

Table I. *Accuracy of Reserve head-spanner checked against Reserve craniostat*

Auricular height in millimetres				
1	2	3	4	
Date ... ..	June 2	June 1		
Skull	Head-spanner	Craniostat	Deviation	cols. 3 and 4
901	107.25	107.25	0.0	
910	125.0	125.0	0.0	
918	108.0	107.75	0.25	
926	118.5	118.25	0.25	
927	106.0	106.0	0.0	
928	113.75	113.75	0.0	
932	110.75	110.5	0.25	
951	112.0	112.0	0.0	
953	110.0	110.0	0.0	
996	114.0	113.75	0.25	
Total deviation	...	...	...	1.00
Average deviation	...	...	...	0.1 mm.

The skulls are drying unmacerated but no appreciable change in dimensions would occur in the 24 hours between measurements.

The slight difference between results is undoubtedly due to the fact that the craniostat has knife-edges whereas the head-spanner has round rods.

Table I gives the data for measuring the accuracy of the Reserve head-spanner. The skulls used in the investigation were in process of drying and not yet macerated but no appreciable change in dimension would occur in the 24 hours between measurement with the two instruments. The table shows that the average difference in auricular height as ascertained with the two instruments is 0.1 mm. less than the instrumental error of the craniostat. Consequently the head-spanner may be regarded as accurate within the limits of possibility of the measurements. The individual difference is 0.25 mm. and in each case the larger figure is obtained on the head-spanner. This is explained by the fact that the head-spanner necessarily possesses rounded ear rods whereas the craniostat is provided with knife-edge rods. Estimating the maximum individual error as five or six times the average error, as was done in the case of Flower's craniometer, an instrument essentially less accurate than the head-spanner, the maximum would scarcely ever exceed 0.6 mm.

#### RELATIVE ACCURACY OF VARIOUS METHODS OF MEASURING AURICULAR HEIGHT

In measuring auricular height, three methods have been adopted. The first is a very simple one which calls for no special instrument and is a modification of the method described fully in Hrdlička's *Anthropometry* (7). A Tasterzirkel is adjusted on the head so that the bulbous extremities of its limbs rest upon the roof of the external auditory passages just within the meatus and the stem of a Gleitzirkel is used to measure the distance from skull vertex to a fixed point on the Tasterzirkel. This dimension, subtracted from the vertical distance between the horizontal passing through the upper aspects of the bulbous extremities and the fixed point mentioned above, gives the auricular height. In this method the adjustment of instruments is done by estimation so that a dimension is obtained at right angles to the Frankfort plane.

The second method is described in Martin's *Lehrbuch* (10, p. 163). One limb of the Stängenzirkel is adjusted to the roof of the left auditory passage and the other, to which the Ohrhöhenadel is affixed, is laid upon the head vertex, the relation of the stem of the Stängenzirkel again being adjusted by eye with reference to the Frankfort plane.

The third method is that described above in connection with our head-spanner.

In order to ascertain the reliability of the several methods I have arranged the following experiment. Using 25 fresh cadavera of a mixed population of Whites and Negroes and of both sexes I have measured the auricular height upon the head-spanner and also by the methods discussed above in association with the names of Hrdlička and Martin. In addition I have measured the height by what I shall call the "old" method. It is based on Hrdlička's method but the measurement is taken from the roof of the ext. aud. meatus, a pelvimeter is substituted for the Tasterzirkel and the third segment of a



Martin's anthropometer for the Gleitzirkel. The measurement simply provided a check upon the Hrdlička method.

Table II *a*. *Comparison of methods*

Auricular height: 25 fresh cadavera; mixed population			
	Average	Standard deviation	Coeff. of variability
"Old" method ...	121.0 ± .666	4.94 ± .471	4.09 ± .391
Hrdlička ...	121.1 ± .666	4.94 ± .471	4.08 ± .390
Martin ...	121.2 ± .688	5.10 ± .486	4.20 ± .401
Reserve head-spanner	122.1 ± .595	4.41 ± .421	3.61 ± .345

Table II *b*. *Deviations of methods from results by head-spanner in mm.*

	"Old" method	Hrdlička	Martin
Total deviation	36.5	34.5	60.5
Average "	1.46	1.38	2.42
Maximum "	8.0	6.0	7.0

Table II *b* gives the results of this experiment. The total deviation of each method from the height ascertained by the head-spanner is recorded without regard to sign. These give average deviations of 1.46 mm. for the "old" method, of 1.38 mm. for Hrdlička's method, of 2.42 mm. for Martin's method. There is no doubt from practical experience that Martin's method is the most difficult to carry out, the most uncomfortable for the individual being measured, and the least satisfactory in result. The exact instruments used are less important than the method employed. This is shown by the fact that our "old" method and that of Hrdlička give practically identical results. The precise maximum deviation is a matter of accident but shows that each of the three methods may be quite unreliable compared with the much more accurate head-spanner.

It has been shown that, so far as individual measurements are concerned auricular height cannot be measured with that degree of accuracy which we should reasonably expect unless a specially designed instrument is used. Anthropologists should therefore not encourage field workers to employ haphazard methods to ascertain auricular height. In justification of this view I present the results of a comparison of reliability of the various methods when applied to a population and not to individuals. Table II *a* gives the averages, standard deviations and coefficients of variability of the three methods checked against the results obtained on the head-spanner. The small variability as ascertained on the head-spanner is intrinsic evidence of the relatively greater accuracy of this instrument and the differences between this coefficient of variability and those of the other methods are measures of the inaccuracy of these methods due to instrumental error. Once again it is apparent that there is no essential difference between our "old" method and that of Hrdlička, the precise type of instrument being less important than the nature of the method employed. It is now plain that, for a population sample, no one of

the three methods under examination gives better results than the other two and any one of them gives an appreciable error in the final result. One cannot too strongly insist upon the standardisation and unification of anthropometric instruments and methods.

#### THE PROBLEM OF SOURCE OF MATERIAL

About ten years ago Pearson drew attention to the fact that a general hospital population cannot be considered representative of the general population of the district (3). Although there may be an obvious difference between the means of these two groups the difference does not extend to the variabilities or correlations. This latter observation might be reasonably inferred. From very numerous series of properly reduced records in this laboratory and from the comparison of these reductions with those made upon similar material by others, notably the Staff of the Biometric Laboratory at University College, we have come to the conclusion that variabilities and correlations have a very distinct "human" value, affected relatively little by stock and only slightly or not at all by sex, age and other features usually emphasised by anthropologists.

The social stratum from which a material is drawn may very readily affect the dimensions, and in certain respects even the proportions of the skeleton. It is therefore unwise to use means obtained from one class in arguments upon another social grade without careful reservations. In the present communication we are concerned, not alone with measurements upon the bony frame, but in addition with determinations upon the soft parts, which, at least in their water and fat content, may be subject to considerable variation. The problem of source of material, therefore, becomes quite important.

The cadavera upon which this investigation is based should be classed as a general hospital population with a distinct criminal and pauper bias. The mean age at death is even less than that for the hospital population given by Blakeman, Lee and Pearson. This is doubtless due in part to the number of deaths from violence (see polygon of age frequency, (12), p. 290)). But this very fact indicates that the material must not be considered as a pure hospital sample; it is a peculiar group characteristic of the anatomical laboratory. Probably the measurements on the skeleton are somewhat under those of the population at large but not so far below this standard as would be those of a pure hospital sample. The same is true of the averages deduced from the soft tissues.

Pearson has drawn particular attention to the effect of want of nourishment and "shrinkage" due to chronic disease (3) in such samples. The "shrinkage" is caused by emaciation which is usually interpreted as loss of weight. The "shrinkage" associated with increasing age, however, probably involves change in the colloidal constitution of the tissues which becomes coarser and expresses water. I feel strongly that in chronic disease such a dehydration also takes place and though I cannot enlarge upon the problem at this time it is of such

paramount importance in this work that we must glance in passing at its probable effect upon the subcutaneous tissues.

#### THE SUBCUTANEOUS TISSUES IN THE LIVING AND THE DEAD

In previous investigations such as those of Czekanowski (4), Anderson (1) and Gladstone (5), it has been either definitely asserted or tacitly assumed that the thickness of the subcutaneous tissues is the same after death as during life. Since the results of this research are to be applied to healthy living persons one must emphatically affirm that the cadaver, in most instances, is not simply the individual after the circulatory and respiratory systems have ceased to function. This communication is not the place in which to enlarge upon this very significant problem which, by its nature, must receive adequate attention upon another occasion. One ought, however, to make passing reference to the matter.

Our interest was aroused in the relation between the healthy individual living and the same person dead by the important fact that the weights of our cadavera almost always are considerably less than those which our experience of the living stripped weight would lead us to expect. Our estimates have been nearly always between 20 and 30 pounds in excess of those revealed by the cadaver scales, a marked exception being the cadaver obtained after a death of violence not involving external haemorrhage. It is apparent that a lingering illness results in emaciation but this emaciation does not appear to explain adequately the considerable loss of weight which our investigation shows. In brief there seems to be a dehydration of the subcutaneous tissues in the last stages of illness. The process of embalming restores the features to a condition more nearly resembling those of life. The amount of fluid used in our embalming method weighs from 16 to 24 pounds according to the size of the cadaver. So far as the scalp is concerned our embalming makes an important difference to the thickness of the soft tissues and this should not be ignored in the present investigation.

Table III. *Effect of embalming upon auricular height*

Nine heads of general population measured fresh and after embalming

	Mean	Standard deviation	Coeff. of variability
Fresh	122.1 ± .798	3.55 ± .564	2.91 ± .463
Embalmed	124.7 ± .832	3.70 ± .588	2.97 ± .472

Table III gives the result of an enquiry into the difference in auricular height induced in the cadaver by embalming. Nine fresh cadavera of our mixed population were measured on admission and again 24 hours after the embalming fluid was introduced into the right brachial artery. Auricular height was chosen because it presents the least disadvantage. Head breadth tends to be exaggerated since the fluid travels up the temporal arteries and often greatly increases this measurement. Head length was discarded because



the cadaver is embalmed while lying upon its back and a relatively small amount of fluid, in consequence, percolates into the tissues over the opisthion which is compressed between the subjacent board and the heavy skull. The vertex of the head, on the contrary, has no large vessels and is subjected to no compression. The second measurement was deferred 24 hours to ensure even percolation of the embalming fluid. As one might expect, the table shows a somewhat greater variability of the measurement in the embalmed cadaver owing to variation in the actual amount of fluid which finds its way to the vertex. But the table also shows that this divergence may safely be ignored in our argument. The difference between the means is 2.6 mm. which represents the increase in auricular height consequent upon embalming. Double this amount should be added to head breadth and head length to indicate the probable true effect of embalming upon these dimensions. The reason for doubling the amount becomes apparent from a study which will be made later in this paper of the variabilities of breadth and length.

A rough check upon this amount of 2.6 mm. is provided in the following manner. We may assume that the total area of the adult male body is in the neighbourhood of two million square millimetres, a figure obtained from Vierordt's quotation from Meeh (14, p. 51). A layer of our embalming fluid 2.6 mm. deep, spread over an area of this size corresponds to a weight of about 13 pounds. Allowing for the fluid which naturally finds its way into the organs and deeper tissues of the body this agrees roughly with our total weight of embalming mixture. It also seems to be warranted by the dehydration of the subcutaneous tissues assumed in our hypothesis.

Of course one may ask why I have not taken a sample of the presumably healthy living population which ultimately finds its way into the dissecting room and checked this up against the dimensions ascertained on our cadavera. Apart from the inherent difficulties of carrying out such an investigation the possible variability of the means of small samples precludes any greater weight being given to the result of work along such lines. Another method would involve measuring the actual thickness of the scalp in the living by a calibrated needle. But this alternative is alike impracticable on account of pain, wounds and deformation of the skin.

For the present then we must rest content with the results now given. The mean auricular height, as ascertained on the cadaver, must be increased by 2.6 mm. to give the probable true mean living auricular height. Breadth on the cadaver must be increased by 5.2 mm. to give the comparable field dimension. Length is the most difficult of all to estimate for the expression of fluid from the soft tissues over the opisthion undoubtedly reduces this dimension. I am inclined to add a further amount of 2.6 mm. (i.e. 7.8 mm. total) to the cadaveric head length in order to obtain the probable true living length.

## THICKNESS OF THE SCALP ON RESERVE MATERIAL

In order to obtain the actual thickness of the soft tissues of the scalp the dimension measured upon the green skull is subtracted in each individual from the corresponding dimension on the cadaver. Mathematical reduction of the remainders so obtained gives the results presented in Table IV. In a former communication I have shown how much the skull shrinks in each of these dimensions in consequence of drying (15). Therefore the figures in this table must not be applied to measurements of the dried skull unless these measurements are corrected for drying.

Table IV. *Thickness of scalp on Reserve fresh material in millimetres*

Type	Number	Dimension	Mean	Standard deviation	Coeff. of variability
Mixed population	69	Length	$4.88 \pm .233$	$2.87 \pm .165$	$58.81 \pm 4.392$
	71	Breadth	$7.29 \pm .230$	$2.87 \pm .162$	$39.31 \pm 2.545$
	21	Aur. height	$6.06 \pm .177$	$1.12 \pm .124$	$19.82 \pm 2.141$
Male White	43	Length	$5.07 \pm .324$	$3.15 \pm .229$	$62.13 \pm 6.014$
	43	Breadth	$7.02 \pm .224$	$2.80 \pm .158$	$40.00 \pm 3.343$
	14	Aur. height	$5.80 \pm .234$	$1.30 \pm .166$	$22.41 \pm 3.144$

The actual number of individuals utilised differs in the several dimensions owing to the fact that certain obvious errors had crept into the records and could no longer be corrected at the time when the statistics were gathered. This accounts for the differences in number of cadavera in the length and breadth series. Since the material obtained during one year is not usually worked up till the following year, and because the Reserve head-spanner was not manufactured until September of 1922, the number of measurements of auricular height is relatively very small. The skulls of the majority of the individuals on which this dimension was obtained with the head-spanner while the cadaver was still fresh and not yet embalmed will not be available until the summer of 1924. At that date it will be possible to review the figures relating to auricular height. But small as the number may be at this time, the averages are not likely to be altered to any practical extent and therefore, instead of holding the entire paper over for two years, it is worth while to publish these results at once. The variability in thickness of the soft tissues involved in the measurement of auricular height is much less than the variability of the soft parts in either length or breadth. This is due, of course, to the fact that only one variable quantity is present, namely the scalp at the vertex. For one could not claim the existence of any practical magnitude in variability of thickness of the soft tissue in the roof of the auditory passage.

The statement just made needs some explanation since it is absolutely opposed to descriptions given by Pearson (2) and Parsons (11) of the relation of the soft tissues to the bony external auditory meatus. The former writer, after an examination of three sections of heads through the meatus concludes that when the ear plug is properly inserted it can scarcely be more than

3 to 4 mm. below the bone. The latter author, on the basis of four tracings of the same region believes that the skin opening is always below the bone but that its distance below varies from 3 to 8 mm. I am not here concerned with head-spanners which give the auricular height from the axis of the ear plug; our instrument determines the height from the upper aspect of the rod. It is well, however, to point out that the material upon which the estimates just quoted are based, was embalmed or at least was dead and that the area is one very frequently distorted by unavoidable post-mortem measures. The finger inserted into the meatus can quite plainly feel the bony margin and the soft tissues are certainly not so thick as either author would lead us to expect. As a matter of fact it is a principle of the use of our head-spanner to draw the rods up to the bony meatal roof immediately within the orifice and it is difficult to believe that the thickness of intervening soft tissues is more than 1 to 2 mm. At any rate the thickness is so small that no appreciable change could occur either in embalming or in emaciation. By far the greatest thickness of soft tissues concerned in auricular height is at the vertex. This is again indicated by the fact that variability in thickness of the soft parts in auricular height is about one half that of the thickness of the soft parts in breadth.

Our results show that the soft parts concerned in breadth are distinctly thicker than those in length. This may be due to the bulk of the temporal muscle which, in certain cases, overlies the Euryon. At least such an explanation has been given by others. I am not convinced that it really has any bearing upon the case for the site of the Euryon is not at all constant and consequently the temporal muscle cannot invariably be included in the dimension. Hence this fact should tend to increase the variability in breadth but the figures show that variability in breadth is much less than variability in length. Nothing is proved by this argument but it at least casts doubt upon the validity of the temporal muscle explanation of the relatively great thickness in breadth. A more reasonable cause for the relatively considerable thickness of soft tissues in breadth compared with length, so far as our cadavera are concerned, is the fact that the body lies upon its back and in consequence there is a tendency for the expression of fluid from the soft parts at the back of the head owing to compression of those tissues between the underlying board and the skull the weight of which, with its contained brain, is considerable.

Again it must be remembered that we cannot give dimensions of the head in the living and we do not know how far these are represented by the dimensions in the cadaver. This problem has been taken up in a separate section of our communication.

For each dimension we have calculated the mean and the variability in a mixed population of both sexes and of White and Negro stocks (Table IV). This is more of theoretical than of practical value. When we have sizeable groups of the female sex and of Negro stock we shall submit figures appropriately dissected. Until then we can give merely the figures for the male



Whites. These, checked up against the corresponding figures for the general population, indicate the effect of admixture of sex and stock together upon average and variability. The general population figures are therefore simply temporary.

It is unnecessary, we think, to compare in detail the results obtained in this work with those given by previous authors for the methods utilised by the different writers vary quite considerably and are often not clearly stated. We must also warn the reader not to accept without caution the quotations of one author from another's work as quite frequently errors seem to have crept into the quotations. Further divers complicating factors enter such as age, sex, state of nourishment of the body, condition of the cadaver, whether fresh or embalmed, and sample of population. We shall content ourselves with comparing the average results for male Whites obtained by us with those given by Czekanowski in his complicated but important communication.

Todd and Kuenzel: length 5.07; breadth 7.02; auricular height 5.80.

Czekanowski:           ,,    7.25;       ,,    6.91;       ,,       ,,    3.43.

Czekanowski does not state from what type of population he derived his data but his methods differ fundamentally from ours. In no case did Czekanowski measure the skull directly: all his skull measurements are hypothetical and are obtained by subtracting the thickness of the soft parts from the directly ascertained dimension on the cadaver. We have already pointed out the danger of error from deformation of the skin in direct determination of thickness of soft parts. Further Czekanowski derived his determination of auricular height from measurements with Martin's method which we have shown to be the most difficult and least dependable of all the methods so far utilised. It is essential, we believe, at this stage to confine attention to a particular sample upon which a complete survey can be made.

#### DIMENSIONS OF THE HEADS AND CRANIA

It will still be many months before the fully dried crania belonging to the series of heads used in this work are all set out ready for service on the Museum shelves. Hence, in emergency, I desire to present for comparison the dimensions with their variabilities ascertained upon the fresh heads and compare them with those of a former standard series of male White dried crania. These figures are gathered together as Tables V and VI. Elsewhere I have commented upon the relatively stable character of human variabilities and the very slight degree in which these differ from sample to sample in spite of statistically significant differences in the means. In actual fact the averages of the 25 crania of our recent series which are now fully dried (shown in Table VII) do differ somewhat from those of Table V but there is no reason to anticipate a corresponding difference in the variabilities.

Now, comparing Tables V and VI, one notes the significant fact that variabilities are less in the dimensions of the cadaver head than in the measure-

ments on the skull. One cannot assume this to be an accident of the samples since it occurs in many different phases of our work where we are comparing the variabilities of any bodily unit with those of the constituent parts of the unit. We are accustomed to speak of this phenomenon in the laboratory as the compensation of the parts in the whole. Its relation to measurements of

Table V. *Reserve cranial dimensions; 167 male White skulls (13)*

	Mean	Standard deviation	Coeff. of variability
Length	181.42 ± .427	8.191 ± .302	4.514 ± .166
Breadth	144.28 ± .296	5.675 ± .209	3.933 ± .147
Aur. height	116.41 ± .252	4.822 ± .178	4.142 ± .152

Table VI. *Cranial dimensions; fresh cadavera; male White only*

Dimension and number	Mean	Standard deviation	Coeff. of variability
Length 43	188.73 ± .797	7.75 ± .564	4.11 ± .299
Breadth 43	153.64 ± .590	5.74 ± .417	3.74 ± .272
Aur. height 16	123.59 ± .695	4.12 ± .491	3.33 ± .397

the skull is demonstrated in an article now being prepared for the press by Dr Pitkin. It is also evident in the precisely comparable figures given by Czekanowski(4) and by Blakeman, Lee and Pearson upon head and skull measurements(3). The paradox is vividly presented by Pearson as a negative correlation between skull diameters and amount of covering flesh.

#### THE COMPUTATION OF DIMENSIONS AND CAPACITY

We originally undertook this work in order to compute cranial dimensions from those of the living head or *vice versa*. In this calculation it is necessary to allow for shrinkage of the skull in drying after maceration as well as for thickness of soft tissues. Corrections for shrinkage have been set forth in a recent communication(15). We shall consider first the computation of average dimensions in a population sample and secondly the calculation of dimensions for individual skulls.

To ascertain what reliance can be placed upon our results for a population sample one must know the dimensions of a series of heads and also the dimensions of the fully dried skulls from the same heads. One can then check the computed cranial dimensions by actual observations. Table VII gives the computed figures for male Whites together with the directly ascertained averages upon the 25 male White crania of our present series which are already fully dried. The greatest difference between calculated and directly determined averages is in breadth, the divergence being 0.9 mm. For length the difference is 0.1 mm. and for auricular height 0.4 mm. One must remember that there will be a slight further shrinkage of these skulls during the coming year for I now find that there may be, though not invariably, a slight shrinkage going on in our crania even after the 12 weeks which we have come to use as a standard

drying period. This would reduce still more the discrepancy for breadth but would rather increase it for height.

Table VII. *Calculation of average head dimensions from measurements on dried skulls—male Whites only*

Average	Length	Breadth	Aur. height
Dimension on 25 dried skulls ...	181.9	145.4	115.7
Shrinkage ... ..	1.8	2.1	1.7
Thickness of soft tissues ... ..	5.1	7.0	5.8
Computed head dimension (cadaver)	188.8	154.5	123.2
Actual " " "	188.7	153.6	123.6
Amount to be added to cadaveric dimension in order to reproduce living dimension ... ..	7.8	5.2	2.6

In order to reconstruct the dimensions of the living head one must add to the cadaveric measurements 2.6 mm. for auricular height, 5.2 mm. for breadth and probably 7.8 mm. for length.

The surprising accuracy with which average dimensions can be computed must not engender a false optimism in results for individual cadavera. We have already shown the great variability in thickness of the scalp. This permits a very considerable deviation between actual dimensions and those calculated from our averages. So long as we deal only with the averages of samples of reasonable size it is probable that the method will be fairly satisfactory. The moment, however, we apply our figures to individual heads, the effect of great individual variability is vigorously demonstrated, even if the individuals are grouped into a series.

From the cadaveric measurements we have calculated the dimensions of the 25 male White crania already dried. Taking round figures we have subtracted from the cadaveric diameters the following amounts for thickness of soft tissues and cranial shrinkage in drying, the figures being based upon Table VII.

Length 7.0 mm.; breadth 9.0 mm.; auricular height 10.0 or 7.5 mm. In auricular height 7.5 mm. is deducted if the cadaveric dimension was ascertained when the body was fresh: 10.0 mm. (i.e.  $7.5 + 2.5$ ) if the body was already embalmed, 2.5 mm. being approximately the increase due to embalming as shown in Table III. The average deviations calculated without regard to sign in these 25 examples are:

L + B + AH 8.8 mm. Length 3.4 mm.; breadth 2.5 mm.; auricular height 2.9 mm.

and the individual ranges are very great:

L + B + AH ranges from	—	15.25	to	+	11.0
Length	„	„	—	7.25	„ + 5.75
Breadth	„	„	—	6.0	„ + 8.0
Aur. height	„	„	—	6.5	„ + 4.5.



When we come to calculate cranial capacity from the computed dimensions we must not even be misled by the  $L + B + AH$  discrepancy of 6.6 mm. This would result in an error of about 50 c.c. in the computation of capacity by any proper regression formula (13, pp. 181-182). We should be quite satisfied if the result were no worse than this. Unfortunately the different diameters are not of equal value in regression formulae and therefore errors of opposite sign in different diameters do not rule each other out but greatly increase the discrepancy of the result. The  $L + B + AH$  figure is naturally obtained by addition of the several deviations having regard to the sign: it therefore gives a fictitious indication of the accuracy to be attained by a regression formula. A truer forecast would be given by addition of the three diametral errors, namely  $3.4 + 2.5 + 2.9$ . This sum of 8.8 mm. error in the average diameters would presage an average error of about 90 c.c. in the calculation of cranial capacity, an error which robs our results of all confidence. On the other hand, by the use of a least square formula, we might hope to attain an average error of about 50 c.c. for in this type of formula the diameters are of more nearly equal value and errors of opposite sign tend to rule each other out. The objection which I have to the least square formula is that it tends to eliminate the essential differences in crania and whereas it should give better average results in principle in a very heterogeneous collection of skulls the individual results would be worse and, if the sample were not very heterogeneous, might be exceedingly bad. To assert that any given sample of skulls is really unselected in any way is to assume a heavy responsibility. The du Chaillu group of West African skulls was selected by the collectors on account of size: that is an easy inference. The Egyptian collections have all been selected in an intangible manner, important factors being the circumstances of exhumation and the necessity of utilising native help. One cannot put one's finger readily upon the influences in this case though there is no doubt of their presence. At an earlier stage of our investigations I was strongly of the opinion that our Reserve male White crania are just about as heterogeneous as they could be, drawn as they are from all the countries of Europe. But our intensive studies of the material from year to year have shattered that illusion completely; we now find that they are indeed quite rigidly selected but by influences entirely unthought of, as I shall demonstrate elsewhere. If then, on the basis of non-selection, one use a least square formula one is apt to encounter quite discouraging results without warning.

In Table VIII I have attempted to illustrate the essential truth of the foregoing statements. Taking a group of ten of the crania of this series we have calculated capacities from linear dimensions using for this purpose the diameters both of the fully dried skulls and of the fresh heads. In the latter calculations the necessary corrections have been made for thickness of the soft parts and for shrinkage during drying. Using Lee and Pearson's least square formula male White reconstructed No. 9 (9), a suitable formula for a heterogeneous collection, we get an average deviation of over 100 c.c. with

either cranial or head diameters. This is unquestionably so inaccurate as to be useless. That is not the fault of the formula, the value of which has been demonstrated by the authors and confirmed in our laboratory (13); it is the logical result of using a general formula upon a selected unsuitable material.

Table VIII. *Calculation of cranial capacity from linear dimensions*

Mean errors in c.c.			
L. and P. Reconstr. male White No. 9	10 heads	Fresh	102.8
	skulls	Dried	104.8
W. R. U. Regression male White No. 5	25 heads	Fresh	101.0
	skulls	Dried	63.0
L. and P. Regression male German No. 8	25 heads	Fresh	64.6
	skulls	Dried	40.8
$\beta$ -group W. R. U. male White No. 5	5 heads	Fresh	31.5
	skulls	Dried	12.1
$\gamma$ -group L. and P. male German No. 8	12 heads	Fresh	57.2
	skulls	Dried	11.1

I have next presented the results given by regression formulæ, using for this purpose our own male White No. 5 (13) and Lee and Pearson's male German No. 8 (9). Now we find that Lee and Pearson's formula gives a much better result than our own. The average error of the Lee and Pearson formula for dried skull dimensions is only 41 c.c., a strikingly good result. The average error of the same formula for fresh head dimensions is only 64 c.c. If we could always obtain this accuracy we should be entirely content. Turning to the results of our own male White formula we find an average error of 63 c.c. for dried skull dimensions and of 101 c.c. for fresh head diameters. At first sight this is very discouraging for it seems to indicate that the formula worked out with the greatest care upon our own material is less serviceable even for our own material than a formula devised from an entirely different population in which the safeguards emphasised in our work were not attainable. But the problem is not so readily disposed of.

In another communication I shall be able to demonstrate that the material upon which these observations have been made is not the material used as the basis for calculation of our formula; different selective influences have been at work. The social turmoil after the war, industrial depression, the subversion of certain social orders, the prohibition amendment to the American constitution, and perhaps most important of all, restriction of immigration and the actual exodus from this country during the past four years have combined to alter the character of our dissecting material. The year 1922 in which all these 25 cadavera, with one exception, were admitted, has brought us a material more closely related on the whole to the crania upon which Ranke made the observations utilised by Lee and Pearson, than to the crania characteristic of the war and pre-war years in this laboratory. This is a bold assertion, and I must ask the reader's indulgence, pending publication of the complete series of observations upon which the statement is made. The material is indeed almost ready for the press. At this time I would mention that the basic prin-

ciple upon which it now appears possible to segregate crania is not cephalic index or race but the definite relation of cranial capacity to the several dimensions of the cranium. We have divided our crania into  $\alpha$ ,  $\beta$ ,  $\gamma$  and  $\delta$  groups. During and before the war the  $\beta$  group was greatly predominant and thus influences most markedly our formula male White No. 5. In 1922 the  $\gamma$  group appears in much larger numbers. This is also the dominant group in Ranke's Altbayerische collection. Hence the better results given in our 1922 material by Lee and Pearson's formula male German No. 8.

Among the 25 crania there are only five of the  $\beta$  group but twelve of the  $\gamma$  group. At the end of Table VIII I have set out the average errors in computation of capacity of these groups, using for the  $\beta$  group our formula male White No. 5, and for the  $\gamma$  group Lee and Pearson's formula male German No. 8. Regression formulae for the other groups have not yet been worked out as we are still in process of identifying the examples. At once the accuracy of the mathematical method of computing capacity is apparent. The error for calculation from dried cranial diameters is well within that of individual direct determination and the error for the calculation from fresh head dimension is small enough to justify further research into the method. The day is not distant when we shall be able to form a fairly exact idea of cranial capacity from head diameters. That reasonable accuracy should be attainable is evident from the demonstration by Blakeman, Lee and Pearson of reasonable probability that the brain-weight of living individuals can be calculated with a mean error of not more than 50 gms. (3).

#### TRANSCERENCE OF OUR RESULTS TO OTHER POPULATION SAMPLES

The next logical stage of this investigation would be the transference of our results to other population samples, a step which cannot be undertaken, as we have shown, without very careful safeguards. It will not suffice to say that, since we have obtained certain results upon a dissecting room population, these dimensions of soft parts can be directly used for the prediction of head dimensions upon, say, a grave-yard sample of skulls. We have confirmed Pearson's assertion of a negative correlation between skull diameters and the amount of covering flesh. When we shall have amassed a considerably larger amount of data it will be possible to compute formulae for deriving skull measurements from those on the cadaver and *vice versa*. Although the formulae will be obtained upon specific populations it should be possible, within limits, to utilise the formulae for other populations. At a later date this will be carried out and we shall be able to test its value by checking very diverse samples against others.

Until such time as this procedure becomes feasible we consider it wise to refrain from any predictions as to the value of the formulae. We content ourselves then with the presentation of such facts as we have so far obtained. These are the necessary preliminary to the further work which has been outlined and we hope that meantime others will endeavour to carry out check



series of observations by which the accuracy of prediction will ultimately be enhanced.

#### SUMMARY

1. We have described a form of head-spanner for obtaining auricular height upon the cadaver and in the living. The instrumental error of this apparatus, as checked against the Reserve craniostat, is 0.3 mm.

2. The instrumental errors have been reviewed for the several instruments necessary to measurement of greatest length and greatest breadth upon the head and upon the skull.

3. The relative accuracy of various instrumental methods of obtaining auricular height are shown in detail.

4. Although full presentation of the thesis must be postponed, it is indicated that the subcutaneous tissues of the cadaver do not accurately represent the condition of the soft tissues during life. The average difference in auricular height between the cadaver fresh and embalmed is 2.6 mm. Consideration of the variabilities of length and breadth suggests that the probable true difference in each of these dimensions is 5.2 mm. This amount should be added to the dimension in the fresh cadaver in order to obtain the approximate breadth in life but for reasons stated in the text 7.8 mm. should be added to length to obtain the real living value.

5. The average thickness of the soft tissues of the scalp has been ascertained for small samples of a general population and for male Whites alone. For male Whites these averages are: height (vertex) 5.8 mm., length (glabella-opisthion) 5.1 mm., breadth (Euryon) 7.0 mm.

6. Shrinkage of the skull in drying having already been ascertained, it is possible, from the measurements on the dried skull, to compute the probable dimensions of the head in the fresh cadaver or in the living. The accuracy for a small sample of male Whites is within 0.9 mm. of the directly ascertained average for each dimension.

For individuals the deviation is naturally greater, but the average accuracy is within 6.6 mm. of the total of the three dimensions as directly determined. This has been shown to correspond to an accuracy in cranial capacity of within 50 c.c.

From the magnitude of the variabilities in thickness of the scalp it is desirable, in the calculation of cranial capacity from head dimensions, to use a formula in which the diametral errors of opposite sign will tend to eliminate each other. It is probable that ultimately least square formulae will give better results than regression formulae because the former tend to diminish differences in the comparative value of the several diameters. It is not possible at the present time to devise such formulae since we have not yet clearly differentiated the various types of skull upon a basis of the relation of capacity to diameters. When this shall have been done and the appropriate least square formula can be applied, there is reasonable probability that we may hope for an average individual error of not more than 50 c.c.

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## RARE CONGENITAL MALFORMATION OF HANDS AND FEET

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H. F., the subject of the deformities to be described, is a railwayman in the permanent way department, who has always been able to perform his work efficiently. He is now 50 years of age.

*Hands:* Both hands show the same condition; the fingers are deviated to the ulnar side at the metacarpo-phalangeal joints which are prominent. There is distinct hollowing of the palms, and the 1st carpo-metacarpal joint is very prominent.

Skiagraph I shows bony condition of the right hand. The 1st metacarpal articulates laterally with the trapezium which is closely attached, if not altogether fused, to the base of the 2nd metacarpal bone. The condition of the left hand is precisely similar.

Skiagraph II shows bony condition of the left hand.

*Feet:* Both feet show the same features. On the dorsum there is a great prominence in front of the ankle joint, the toes are deviated outwards. The plantar aspect shows a very high plantar arch more correctly described as a hollow. The condition is an exaggerated form of pes cavus.

Skiagraph III shows the bony condition of the left foot. The scaphoid stands up prominently on the dorsum, and its inferior border ends in a rather sharp wedge. The internal cuneiform is peculiar in shape, and seems partially fused to the base of the 1st metatarsal. The angle formed by the junction of the longitudinal axes of the os calcis and the 1st metatarsal is almost a right angle.

H. F. has 2 sons and 1 daughter. The elder son's hands and feet are normal. The daughter has normal hands, and moderately high plantar arches. The younger son, aged 15 years, has well marked plantar arches in both feet.

Skiagraph IV shows bony condition of right foot in the younger son.

The parents of H. F. are alive, and their hands and feet were examined. The father was normal. The mother has very high plantar arches in both feet but no obvious abnormality of the hands. A sister has well marked plantar arches and normal hands. The feet and hands of two brothers who live in the locality are quite normal. One brother showed abnormal increase of movement in the left thumb, but an X-ray plate showed the articulations to be quite normal.





Skiagraph I



Skiagraph II



Skiagraph III



Skiagraph IV

*Comments:* The variations in form and structure of the hands and feet in this case are in some degree correlated, and so far as the feet are concerned inherited and passed on to the third generation.

Evidently the condition arises in the germ cell: there is no suspicion that it is pathological or acquired.

Dwight(1) does not mention a similar condition of the hand in his monograph, and Dr Thurston Holland, of Liverpool, with his great experience of radiography has not seen it either, so that it may be considered excessively rare and worthy of record.

Partial fusion of the internal cuneiform with the base of the 1st metatarsal has been previously described by Thurston Holland(2), but I can find no reference in the literature available to me to the peculiar shape of the scaphoid with its wedge shaped border. Sir Arthur Keith, who has seen the prints, considers the condition one in which both bone and muscle are involved.

The question as to how far the variations in the hand are homologous with those in the foot in this case I would prefer to leave to expert anatomists.

I am greatly indebted to Dr Edward Fox of Warrington for the skiagraphs.

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## A NOTE ON A CASE OF BIFID PENIS

By ALEXANDER LIPSCHUTZ,

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A CASE of bifid penis with penile hypospadias is described by Pires de Lima (1), in a man of 58 years of age. In this case the body of the penis is said to be short and wide, ending in a double well developed, though imperforate, glans. The urethral opening is present on the ventral surface of the organ, at a distance of 4 centimetres from its distal end, and 2 centimetres from the scrotum. This malformation, according to the patient, does not affect his sexual functions. He is married, and is the father of five children.

Another case of bifid penis with hypospadias is described in *Rassegna di Studi Sessuali* (2), but in this case the separation of the glans is less complete. This man is said to be sexually normal.



Fig. 1

A case of bifid penis which involves both the body and glans, with possibly a hypospadias, is shown in the accompanying photographs, which were taken of a patient in the Surgical Clinic of the University of Dorpat. In this case the body and glans show complete separation into two parts, giving the appearance of a double penis. The body and glans of each half appear of usual length, but together are slightly wider than normal. The scrotum and testicles

are normal in size and position, and this taken in conjunction with the secondary male character of the triangular-shaped distribution of the pubic hair, would indicate that the patient was sexually normal.

It is to be regretted that no other details of this case are available, as the hospital archives were lost during the war and revolution.

I am indebted to my colleague, Professor K. Konik, director of the Surgical Clinic of Dorpat University, for permission to publish the photographs.

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## ON THE HOMOLOGIES OF THE SKULL OF THE CYCLOSTOMATA.

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IN a recent work (Allis, 1923), I have been led to conclude that the polar and trabecular cartilages of the Gnathostomata are, respectively, the pharyngeal elements of the mandibular and premandibular arches; and in several earlier works (Allis, 1918, 1919, etc.) I have sought to establish that the lateral wall of the pars jugularis of the trigemino-facialis chamber of the Gnathostomata, wherever present, and the hyomandibula of the Ganoidei, Crossopterygii and Teleostei are, respectively, special developments of the branchial-ray bars of the mandibular and hyal arches. In the present article I shall assume these conclusions to be correct, and attempt to interpret the skull of the Cyclostomata in accordance with them.

The parachordals of the Cyclostomata are short plates lying one on either side of the anterior end of the notochord. The tip of the notochord is exposed between their anterior ends, and lies in the horizontal plane of the posterior portion of the chorda, without flexure either upward or downward. The parachordals are continued forward by the so-called trabeculae, which lie in the plane of the parachordals and diverge slightly from each other, and they, in turn, are continued anteriorly by the so-called palatines. A zone of so-called soft cartilage may intervene between the trabecula and palatine of either side, this suggesting that the two elements are of independent origin. Arising from this intervening zone in *Myxine* (Cole, 1905), and from the corresponding part of the continuous bar in *Bdellostoma* (Ayers and Jackson, 1901), there is a short mesially directed process which fuses with the lateral edge of the so-called hypophyseal plate, and the nervus opticus runs outward across this part of the trabeculo-palatine bar. In larvae of *Petromyzon* (Parker, 1883) the conditions differ only in that there is no mesially directed process arising from the trabeculo-palatine bar, and that the nervus opticus crosses the dorsal surface of the bar slightly posterior to what would seem to be the line of fusion of its two components. The so-called palatines extend forward to the ethmoidal region and there fuse with each other in the median line. The pituitary body lies in the space enclosed between the trabeculae.

The so-called trabeculae and palatines of these fishes are thus, in their topographical relations to each other, to the parachordals, to the pituitary body, and to the optic nerves, strictly comparable to the polar and trabecular cartilages of the Ganoidei and Teleostei, and as their relations to the veins



and arteries of the region are also in accord with this assumption, as shown immediately below, they will hereinafter be so referred to.

The only detailed descriptions that I have at my disposal of the veins and arteries of this region are those by Cori and Favaro. According to Favaro (1908, pp. 365-366), Vogt (1889-94) describes a *circulus cephalicus* in *Petromyzon fluviatilis*, and Jammes (1904) one in *Petromyzon marinus*. Cori (1906), however, did not find this *circulus* in the *Ammocoetes* of *Petromyzon fluviatilis*; Favaro says that Sterzi (1907) did not find it in the specimens of *Petromyzon* examined by him, which are referred to as the "einheimischen *Petromyzonten*" and hence probably included both *Petromyzon fluviatilis* and *Petromyzon marinus*; and I do not find it in a 60 mm. specimen of *Entosphenus tridentatus*. This *circulus* is thus certainly not a constant feature in these fishes.

Cori calls the lateral dorsal aorta the *arteria carotis dorsalis*, while Sterzi (quoted from Favaro) calls it the *carotis interna*. Cori says of it (1906, p. 30): "Im Bereiche der Augen jedoch rücken sie (the dorsal carotids) an die mediane Kante der Trabekeln, welche sich vermöge ihrer lyraförmigen Krümmung mit ihren Vorderenden von der Chorda mehr und mehr entfernen. Eine kurze Strecke vor den Enden des Trabekels überkreuzt jederseits die Carotis denselben und ist dann als ein nahezu gerade verlaufendes Gefäß bis zum Geruchsorgan zu verfolgen." The use, here, of the word "überkreuzt" would certainly seem to mean that the carotid (lateral dorsal aorta) ran upward along the mesial surface of the polar cartilage (Cori's trabecula), and then crossed its dorsal surface, but, as will be later shown, this is either exceptional in these fishes or is a feature of *Ammocoetes* and not of the adult *Petromyzon*.

Having reached the anterior end of the polar cartilage in the manner above set forth, the lateral dorsal aorta of *Ammocoetes* is said by Cori to separate into three branches. Two of these branches are the anterior and posterior cerebral arteries. The third branch is called by Cori the *vena spiraculi*, and of it he says (1906, p. 31): "Die Abzweigung der *vena spiraculi* aus der *Carotis dorsalis* findet an der Stelle statt, wo letzere das Ende des Trabekels erreicht hat und noch medial von diesem liegt. Die *Spiracularvene* schlägt sich dann um die Trabekelspitze herum und nimmt ihren Verlauf lateral von dem Trabekel in nahezu gerader Richtung nach rückwärts..."; and in the figure that accompanies this description, the lateral dorsal aorta and the *vena spiraculi* both seem to lie internal to shading that represents the polar cartilage. The vein then turns downward and enters the velum, where it is connected, by capillary vessels, with the *arteria spiraculi*, which carries arterial blood. These two vessels, the *vena* and *arteria spiraculi*, are therefore considered by Cori to represent an aortic arch, and as it lies next anterior to the hyomandibular (hyal) arch, it is said to be the mandibular aortic vessel, and the velum, which lodges it, to be a persisting portion of the mandibular arch. The *arteria spiraculi* of Cori's descriptions is, accordingly, the afferent artery of this arch, and the *vena spiraculi* the efferent artery. The hyomandibular (spiracular) cleft, before its obliteration, should therefore have lain immediately posterior to the

velum, and both Cori and von Kupffer (1900) consider it to have had that position.

Anterior to this mandibular aortic arch, Cori describes (*loc. cit.* pp. 21 and 34) still another arterial connection between the dorsal and ventral arterial trunks. It lies in the margin of the upper lip, is formed by the so-called ramus labialis communicans together with terminal branches of the arteria lingualis and the arteria facialis (lateral dorsal aorta), and Cori suggests that it quite probably represents a premandibular aortic arch.

In the specimens of *Petromyzon* described by Sterzi, a radically different arrangement of the lateral dorsal aorta and efferent mandibular artery is found. According to him (see Favaro, 1908, p. 366) the lateral dorsal aorta (his carotis interna) becomes imbedded, in the region of the pituitary fossa, in the perichondrium of the basis cranii, and while there separates into two branches, one of which enters the cranial cavity and is the arteria cerebralis. The other and larger branch continues "in der Dicke der Basis cranii nach vorn fort, umfasst medialwärts den Recessus hypophyseos und beigt dann abwärts und nach vorn um, um in den vorderen Kopfteilen zu enden." The lateral dorsal aorta of the specimen, or specimens, here referred to thus evidently crosses the ventral edge of the polar cartilage, and the efferent mandibular artery must necessarily join it at some point actually, or morphologically, ventral to that cartilage.

In a 60 mm. specimen of *Entosphenus tridentatus*, I find conditions strictly similar to those described by Sterzi, the so-called perichondrium of his descriptions being a thick layer of fibrous tissue that extends from one polar cartilage to the other, immediately internal to the lining membrane of the roof of the pharyngeal chamber, and the lateral dorsal aorta issuing from this tissue, ventral to the polar cartilage, before receiving the efferent mandibular artery.

It is thus seen that, as described by Cori, the lateral dorsal aorta and the efferent mandibular artery of the Ammocoetes of *Petromyzon fluviatilis* have to the polar cartilage the relations that the corresponding arteries of the Selachii have to that cartilage, while in the specimens of *Petromyzon* examined by Sterzi, and in *Entosphenus tridentatus*, these same arteries have to the polar cartilage the relations that they have in the Holostei and non-siluroid Teleostei (Allis, 1923). Furthermore, this selachian disposition of these arteries in Ammocoetes exists without the presence of a circulus cephalicus, which I considered of prime importance in this connection. It may therefore be that there is error here, either in Cori's descriptions or in my interpretation of them. Otherwise it must be, either that these arteries vary in this important respect in different individuals or species of *Petromyzon*, which seems improbable, or that the lateral dorsal aorta of these fishes shifts from the mesial to the lateral surface of the trabeculo-polar bar during metamorphosis, as it does at a certain stage of development in *Amiurus* (see Allis, 1923). In the descriptions of *Amiurus*, however, the efferent mandibular artery is not described, and there



is nothing to indicate that it joins the lateral dorsal aorta dorsal, instead of ventral, to the trabeculo-polar bar. Aside from these relations of these two arteries of *Ammocoetes* to the polar cartilage, their general arrangement and distribution resembles that in *Polypterus* and the adult *Amiurus* (Allis, 1908 *a*, 1908 *b*) much more than it does that in the *Selachii*.

The pharyngeal basket may now be considered. This part of the cranial skeleton of these fishes has usually been considered to be formed by the fusion of a quadrate, or pterygoquadrate, with certain parts of the cartilaginous bar of the hyal arch, but the course of the ramus maxillo-mandibularis trigemini ventral, instead of dorsal, to the so-called quadrate has frequently been cited as unfavourable to the inclusion of that element in the basket. The basket of the *Petromyzontidae* is connected with the cranium by two dorso-mesial processes, both of which are assigned to the pterygoquadrate; the epihyal and ceratohyal are considered to be represented in the so-called styliform process, which projects ventro-posteriorly from the hind edge of the subocular portion of the basket; and the anterior dorso-ventral bar of the branchial basket to be formed by the extrahyal. The basket of the *Myxinoidea* is connected with the cranium by three processes, the anterior two being assigned to the pterygoquadrate and being considered to be the homologues of the two processes of the *Petromyzontidae*, while the posterior one is assigned to the hyal arch and is called by Parker (1883) the *hyomandibula*. Sewertzoff (1913) considers the entire pharyngeal basket of *Petromyzon* to belong to the mandibular arch, and the "*hyomandibulare + hyoideum*" to be represented in the extrahyal of Parker's descriptions. The ethmopalatine and prepalatine of Parker's descriptions are said by Sewertzoff to represent a first premandibular arch, the posterior upper labial cartilage to represent a second premandibular arch, and the anterior upper labial a third such arch. The mouth is said to be terminal, and to be bounded by elements that lie anterior to the third premandibular arch.

Neither of the above mentioned interpretations of the basket is wholly in accord with its relations to the *nervi trigeminus* and *facialis*, and my work leads me to suggest that the pharyngeal basket of these fishes has been developed from what I have described, in other fishes, as the branchial-ray bars of the mandibular and hyal arches. In the *gnathostome* fishes the tissues from which the branchial-ray bars of the mandibular arch are developed lie, primarily, on either side of the ramus maxillo-mandibularis trigemini slightly distal to its ganglion. They are primarily wholly independent of the branchial bar of the arch, and they later fuse with each other both dorsal and ventral to the *nervus trigeminus*, and then with the cranial wall both dorsal and ventral to the *vena jugularis*. The tissues that lie anterior to the nerve thus give origin to the parasphenoidal leg of the alisphenoid, which has its ventral attachment at the anterior end of the polar cartilage; the tissues that lie posterior to the nerve giving origin to that part of the lateral wall of the *pars jugularis* of the trigemino-facialis chamber that lies between the *nervi trigeminus* and *facialis*, and has its ventral



attachment in the region of the hind end of the polar cartilage. In the hyal arch the corresponding tissues lie on either side of the ramus hyomandibularis facialis, and, in the Holostei and Teleostei, give origin, respectively, to the pre-facialis and postfacialis portions of the teleostean hyomandibula. In Polypterus and the Chondrostei the prefacialis tissues alone undergo chondrification, and form the hyomandibula of those fishes, which is thus the equivalent of one half only of the hyomandibula of the Holostei and Teleostei.

In the Amphibia these same tissues are found, but the mandibular portion there fuses with the quadrate, instead of with the cranium, and forms its ascending and otic processes.

Let it be assumed that these same branchial-ray tissues were present in the mandibular and hyal arches of the Cyclostomata. When, in the mandibular arch, the pharyngeal element swung upward and forward into the plane of the parachordals, the tissues that form the branchial-ray bars of the arch would be pulled somewhat away from the epal element, to which they were primarily related, and would lie slightly lateral to the pharyngeal element, which becomes the polar cartilage. Let it be further assumed that they did not then grow upward to any extent, but simply fused with each other both dorsal and ventral to the ramus maxillo-mandibularis trigemini, and then, having undergone chondrification, fused, by their ventral ends, with the polar cartilage, the latter cartilage having already fused with the parachordal and so become part of the cranium. That part of the cartilage that forms the anterior fusion with the cranium would then lie between the nervus ophthalmicus profundus and the ramus maxillo-mandibularis trigemini, and would correspond to the parasphenoidal leg of the alisphenoid (processus ascendens quadrati) of the gnathostome fishes, while the cartilage that forms the posterior fusion would lie between the nervi trigeminus and facialis and would correspond to the lateral wall of the trigemino-facialis chamber (processus oticus quadrati). This would fully account for the relations of the nerves to this part of the basket, and that the basket was primarily wholly independent of the cranium is shown by the conditions that I described in what was probably a 12 cm. specimen of *Bdellostoma*, but was said, doubtless by typographical error, to be a 12 mm. one, for in that specimen the basket was wholly free from the cranium. And that it is by their ventral, and not by their dorsal ends that the branchial-ray bars here fuse with the cranium is shown by comparison with *Necturus* and the tadpole of *Rana*, for in both these amphibians the dorsal ends of these two bars either abut against or fuse with the cranium ventral to the foramina of the related nerves, and in both of them the nervus ophthalmicus profundus runs downward posterior to the processus ascendens quadrati, and the ramus maxillo-mandibularis trigemini forward dorsal to it; which, while apparently exactly the reverse of the relations of these nerves to the process of *Ammonoetes*, is, nevertheless, morphologically exactly the same (see Allis, 1903, pp. 326-327).

In the hyal arch, the anterior branchial-ray bar has undergone chondrification in the Myxinoidea, and forms a third connection of the basket with

the cranium. It lies posterior and dorsal to the nervus facialis, that nerve running posteriorly ventral to it and then turning outward and forward around the hind edge of the basket. This process thus has to this nerve the relations of the prefacialis portion of the teleostean hyomandibula, and it must therefore be that it is the dorsal end of the branchial-ray bar, instead of its ventral end, that has here fused with the cranium; and that such is the case is furthermore indicated by the conditions shown in one of Cole's figures of *Myxine* (Cole, 1909, fig. 1), the process there fusing with the lateral wall of the auditory capsule near the middle of its height. The postfacialis portion of the hyomandibula would then probably be represented in that little posteriorly directed process on the hind edge of the bar that forms the posterior boundary of that perforation of the basket that is called fenestra 3, for the nervus facialis runs downward and forward dorso-anterior to it. The remainder of the basket would then probably be developed wholly from the branchial bar tissues of the hyal arch, and not from the branchial-ray tissues.

In *Petromyzon*, this third connection of the basket with the cranium does not exist, and it is probable that neither of the branchial-ray bars of the hyal arch chondrify. The course of the nervus hyomandibularis facialis should give positive indications as to this, but I do not find it satisfactorily described. Parker says (1883, p. 415): "The facial nerve emerges behind the pedicle and then passes to the inside of the forking cartilage"; and this so-called forking cartilage would seem to be the epi-ceratohyal of his descriptions, for in his Plate XVIII, fig. 5, he shows the nerve running ventrally internal to it. This relation of nerve to cartilage is, however, the direct opposite of what is always found in the gnathostome fishes, provided the cartilage is the epi-ceratohyal. If it is of mandibular, instead of hyal, origin, the position of the nerve internal to it would be normal, and this is possibly what led Sewertzoff to assign it to the mandibular arch. Fürbringer, however, says (1875, p. 67) that this nerve of *Petromyzon* runs forward between the eye and the subocular arch, and hence external to the epi-ceratohyal; and Johnston (1905, p. 161) says that, after giving off several branches, the main trunk of the facialis "gains the outer surface of the branchial cartilage," and this latter cartilage must evidently be some part of the pharyngeal basket. It therefore seems fairly certain that this nerve of *Petromyzon* runs outward posterior to the post-trigemini connection of the pharyngeal basket with the cranium, and then turns ventro-anteriorly external to the epi-ceratohyal of Parker's descriptions. There is, accordingly, no homologue of the prefacialis portion of the teleostean hyomandibula in this fish, and if the postfacialis portion is present it must be represented in some part of the extrahyal of Parker's descriptions.

The relations of the two or three processes of the pharyngeal basket of the Cyclostomata to the cranial nerves are thus in accord with their being the branchial-ray bars of the mandibular and hyal arches. Their relations to the venae capitis media and capitis lateralis are, however, not the same as those of the corresponding processes of the gnathostome fishes. In the latter fishes



these two veins unite in variable manner to form the vena jugularis, and that vein always traverses the pars jugularis of the trigemino-facialis chamber, when that part of the chamber is present, thus lying between the points of fusion of the dorsal and ventral ends of the branchial-ray bars with the cranial wall. In the Ammocetes of *Petromyzon fluviatilis* the points of fusion of the ventral ends of the bars lie between the two veins, as described immediately below. What the relations of these processes to the veins are in the Myxinoidea I do not know, for I find no description of the veins in Myxine, and I have not been able to consult Jackson's (1901) descriptions of them in Bdellostoma.

It may here be stated that the trigemino-facialis chamber of my descriptions of Bdellostoma (Allis, 1903), which was said to lie in the membranous lateral wall of the cranium, is, in reality, only the pars ganglionaris of that chamber, for the venae capitis media and capitis lateralis both lie wholly external to it. The chamber of this fish, and hence probably also that of others of the Cyclostomata, thus lacks a pars jugularis, as it also does in many of the Gnathostomata. When the work above referred to was published, I had not yet determined that there are two distinctly different parts to this chamber of fishes, and that they are frequently completely fused with each other, as in *Amia*.

The vena capitis media of Ammocetes, which is the cephalic portion of the primitive vena cardinalis anterior, is said by Cori (1906) to begin along the edge of the upper lip in a vein called by him the vena facialis. Running posteriorly this vein receives the vena veli dorsalis, coming from the velum, then the so-called vena mandibularis, which lies parallel to, and immediately anterior to, the "Pseudobranchialrinne," and then passes ventral to the pharyngeal basket and ventral to the dorsal end of the glossopharyngeus branchial bar, and unites with the vena capitis lateralis to form the vena cardinalis anterior. As the vein traverses the otic region it lies along the lateral surface of the aorta, in a fold of the epidermis that projects ventrally into the pharyngeal chamber, thus lying definitely ventral to the chorda; this doubtless accounting for the fusion of the mandibular branchial-ray bars with the parachordal dorsal, instead of ventral to the vein. Immediately anterior to the otic capsule the vein gives off a so-called vena cerebri media, which runs upward lateral to the trabeculopolar bar, between the trigeminus and facialis ganglia, and falls into the vena capitis lateralis, thus forming a connecting branch between these two veins which corresponds to the branch found in similar position in the Gnathostomata. In Ammocetes, however, the vena capitis media persists posterior to this point, while in the Gnathostomata it aborts from this point to the point where the next posterior communicating branch to the vena capitis lateralis is given off. In Cori's figure of these veins it is, however, to be noted that there is apparently a break in the vena capitis media posterior to the communicating branch above referred to, and it is not fully evident how the blood from his vena facialis reaches the proximal end (base) of the vena capitis lateralis. No pituitary vein is described, the pituitary body doubtless being drained, as it is in *Amiurus* (Allis, 1908 b), by intracranial veins.



The vena capitis lateralis is said to begin, at the anterior end of the brain, as the vena cerebri anterior, to run posteriorly dorsal to the eye and to the ophthalmicus, trigeminus and facialis ganglia, to receive the communicating branch from the vena capitis media above described, and then, at the hind end of the otic capsule, to receive a large vena cerebri posterior. The capitis lateralis then turns ventrally between the glossopharyngeus ganglion and the latero-sensory ganglion of the vagus, and then posteriorly ventral to the latter ganglion but apparently dorsal to the remainder of the ganglion of the vagus, though this is not definitely stated. The vein here passes dorsal to the dorsal end of the branchial bar of the glossopharyngeus arch, and then separates into two parts, both of which turn downward and join the vena capitis media to form the vena cardinalis anterior, which runs posteriorly dorsal to the dorsal ends of the remaining branchial bars.

The vena capitis lateralis of this fish thus lies ventral to the latero-sensory ganglion of the vagus, but dorsal to all components of the more anterior ganglia. In the gnathostome fishes this vein lies dorsal to all the components of the acustico-facialis ganglion, but ventral to the latero-sensory components of all the other cranial nerves, the rami ophthalmicus superficialis and buccalis being considered to belong to the trigeminus nerve. There should then, if the relations of this vein to the latero-sensory ganglia is of morphological importance, be no latero-sensory component in either the ophthalmicus, trigeminus or glossopharyngeus ganglia of *Petromyzon*, and this is in accord with Favaro's (1910) statement that all the fibres distributed to the latero-sensory organs on the head of this fish issue from the cranium with the nervus facialis and form a separate and independent ganglion which lies beneath the otic capsule. From this ganglion a nervus lateralis anterior arises and separates into three branches, a ramus buccalis, an anastomosis gangliorum lateralium (ramus recurrens facialis), and a nerve which is said to join and accompany the nervus ophthalmicus profundus and innervate a line of latero-sensory organs which is considered to be the homologue of the supraorbital line of the Gnathostomata. Allcock (1898), however, finds this latter line of organs innervated by the ramus buccalis, in the *Ammocoetes* of *Petromyzon planeri*, and I so find it innervated in *Entosphenus tridentatus*. It is therefore possible that the so-called supraorbital and suborbital lines of organs of these fishes are both innervated by a nerve that is the homologue of that branch of the ramus mandibularis externus facialis of the Holostei and Teleostei that innervates the cheek lines of pit organs of these fishes, and that, like the horizontal cheek line of *Esox* (Allis, 1898, p. 441 and 1904, fig. 6), these lines of organs of *Petromyzon* have been shifted bodily forward to the positions they actually occupy.

There is thus nothing, either in the veins or arteries of the region, or in the peripheral distribution of the cranial nerves, that is unfavourable to the interpretation, above proposed, of the skull of these fishes. The hypophyseal canal must have lain, primarily, between the trabeculae (pharyngopremandibulars)

and morphologically dorsal to them (Allis, 1923), but it has been pressed downward by growth of overlying parts of the brain, and hence has, in *Petromyzon*, a curved course, and lies, in the middle of its length, ventral to the horizontal plane of the trabeculo-polar bars. In *Myxine*, the lowest part of this curved canal apparently came in contact with the roof of the pharyngeal chamber, and, the intervening tissues then breaking down, the naso-pharyngeal canal arose. The hypophyseal plate, which underlies this canal, is then simply an intertrabecula pushed downward into a more ventral position, and the two short processes that connect it with the trabeculo-polar bar are the homologue, together, of the preclinoid wall of the *Gnathostomata*; as already suggested in an earlier work (Allis, 1903, p. 324).

The vena facialis is said by Cori to be in capillary relations with the ramus labialis communicans, which, as already stated, is an arterial vessel lying along the margin of the upper lip and forming a connection between the ventral and dorsal arterial trunks; and Cori suggests that this latter vessel may represent a premandibular aortic arch. The lateral labial cartilage of *Bdellostoma* has a similar course in the lip of that fish, and if there is here an arterial vessel similar to that in *Ammocoetes*, which seems exceedingly probable, the labial cartilage would have the relations to it of the branchial bar of the arch. This cartilage is fused ventrally with the anterior end of the basal plate, and its dorsal end is in close relation to the anterior end of the cornual cartilage. The latter cartilage arises from the anterior end of the trabecula (so-called palatine), and extends forward in a curved line. If, therefore, the trabecula is the pharyngeal element of the premandibular arch, the cornual and lateral labial cartilages would have the relations to it of the epal and ceratal elements of the same arch, and the tentacular cartilages would be related branchial rays. The mandibular cleft should then lie posterior to this arch, between it and the velum (mandibular arch), and von Kupffer (1900) here describes a longitudinal groove in the roof of what he calls the primary mouth cavity, the groove extending from the region of the optic vesicle to the hyomandibular visceral pouch. Von Kupffer refers to this groove as a pouch, or pocket (*Tasche*), and the evaginations of the branchial clefts are all referred to by the same term (*Kiementasche*). He does not suggest that the prevelar pouch represents a mandibular cleft, but whatever its nature may be, if the arteries and cartilages above referred to represent the premandibular arch, the mouth would be a median terminal opening lying between the premandibular arches of opposite sides.

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# MALFORMATION OF THE DIAPHRAGM IN A DOG

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AND

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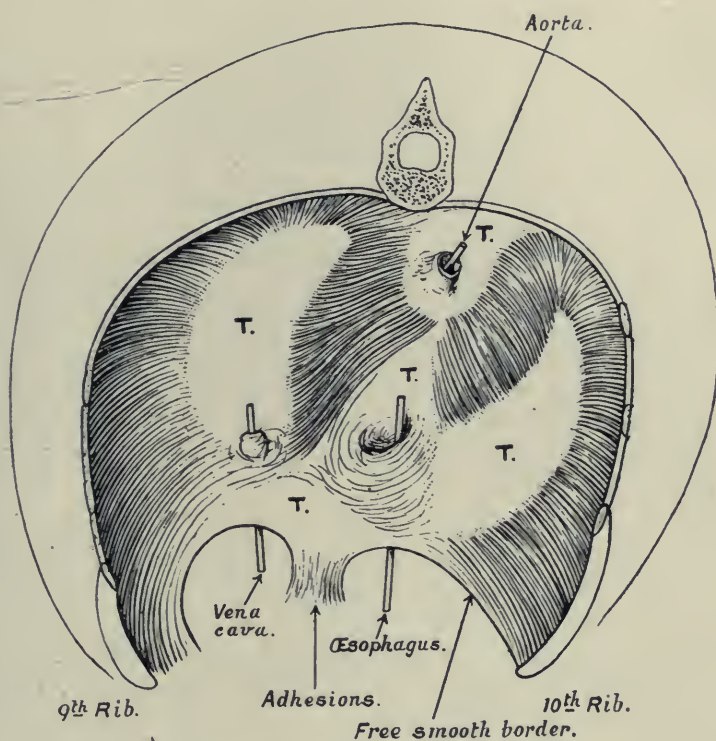
*Physiological Department, University College, Cork.*

ON opening the thorax of a pregnant bitch for the purpose of doing some experiments with the heart-lung preparation, we were at once struck by the abnormal appearance of things. The guiding finger behind the sternum met with no resistance such as is usually offered by the diaphragm after the xiphisternal cartilage is split. On completing the sternal cut the left lobe of the liver presented itself in the upper part of the left side of the thorax, and between it and the thoracic wall, as high as the level of the third rib, some coils of small intestine were seen; the heart was pushed to the right; there had been no occasion to palpate the apex-beat prior to opening. The pericardial sac was complete, and the heart rested in a pit on the upper surface of the liver, partly on the right lobe and partly on the left, without the intervention of a diaphragm. It was held there by a short fold of pericardium attached to the anterior border of the diaphragm, behind, where the liver was also adherent. It was obvious at once that there was a defect in the diaphragm, which was then carefully examined.

The diaphragm presented a concave anterior border, for the most part free, but adherent to the liver behind the heart. The opening of the vena cava was about one inch behind this border, and the oesophageal opening about two inches behind it to the left of the vena cava (fig. 1). There was a large gap between this border and the front wall through which there was prolapse of a great part of the liver, the stomach and the small intestine into the thorax. The right lobe of the liver was adherent to portions of the anterior edge. This concave edge was limited on the left by attachment to the tenth costal cartilage and on the right to the ninth. The posterior portion of the diaphragm was perfectly formed and there was complete closure there.

The anterior tongue of the central tendon of the diaphragm ends in the pericardial fold. The central part of the diaphragm through which passes the oesophagus is thick and muscular; and while this is normal in the dog there is, however, an excess of muscle in this area; the vena cava opening is also surrounded by muscle but in thinner layers than the oesophageal. The chief tendinous parts are two lateral portions as seen in fig. 1. Blair describes many accessory muscle slips in the tendon of the human diaphragm (*Journ. Anat.* LVII. Part III, p. 214, 1923). In this animal's diaphragm there certainly was abundance of muscle which looked like compensatory growth. The ribs and conformation of the thorax were normal.

The left lung was considerably pressed upon by the abdominal viscera;



T.T. Show tendinous patches.

Fig. 1. Drawing of the upper surface of diaphragm.

the edge of the liver compressing the vessels at the root and causing considerable congestion of the base and portions near the root. This lung weighed 85 gms. the right lung weighed 107 gms.

*Remarks:* Evidently the malformation here affected that portion of the diaphragm which is developed from the septum transversum. The connective tissue which lies over this part in the embryo for some reason did not develop. The possibility of a traumatic injury to the diaphragm may, we think, be excluded, from the shape of the portion which was intact and its limitations. The parts formed from the mesentery, the pleuro-peritoneal membrane, were, as stated, perfect, and the gap corresponded exactly with that part derived from the septum transversum. The gastro-hepatic omentum with the foramen of Winslow were in their normal condition, though of course dragged to the left and upwards with the stomach.

The unusually large gravid uterus, containing five foetuses near term must have aggravated the condition, being probably the chief factor in the obstruction to the pulmonary circulation.

We have, unfortunately, no present opportunity of going extensively into the literature of this subject, but we consider the condition of sufficient interest to be reported.

## THE SCALENUS MEDIUS

By B. S. NAT, M.B., CH.B.

THE Scalenus Medius is described in text-books of anatomy (Quain, Gray, and Cunningham) in an indefinite and vague manner. In describing its relations the text-books do not seem to be clear about its general shape and its surfaces. Further there is no attempt made to define its relations with the first levator costae muscle—a clear conception of which is essential for understanding the shape and relations of the scalenus medius. I am giving here a description of the muscle as I found it in all the specimens which I examined for this purpose in University College, Dundee.

The scalenus medius is best described (from the point of view of descriptive anatomy) as a flat muscle folded on itself, making a sort of prism with one side (inner) hollowed to form a deep gutter: so in a transverse section it is as shown in the figure. It arises by slips from the anterior aspect of the true transverse processes of the lower six cervical vertebrae (not from the *tips* of these transverse processes, which form the posterior tubercles). Occasionally a thin “areolar-tissue-like” slip may be seen passing to the transverse process of the atlas. The upper slips of origin are mostly tendinous and thin, but the lower ones are of considerable thickness and have fleshy fibres mixed with tendinous ones. These slips lie immediately behind the issuing spinal nerves.

The disposition of the muscle shown in the figure, where it seems to be wrapped round the transverse process and posterior tubercle, is brought about by the fibres of the upper slips of origin—which would form the lateral border if the muscle were flattened out—passing down behind the transverse processes below and lying against their posterior surfaces: they may be attached to these by dense areolar tissue but never take origin from them. The slip from the 4th (or 5th) transverse process generally forms the outermost part of the muscle and its lateral border. This border is the result of the folding back of the muscle. The upper two (or three) slips incline backwards as they descend to form the posterior (or postero-external) surface.

Looked at from this point of view the shape and relations of the muscle can be very definitely described. It has three surfaces: a concave medial surface lying in contact with the posterior tubercles and posterior inter-transverse muscles. The attachment of splenius colli, transversalis cervicis, and cervicalis ascendens to the cervical transverse processes is in relation with the postero-internal edge of the muscle. It should be noted that this surface is practically non-existent in the upper part of the muscle and hence the slips of origin of the levator anguli scapulae are, generally speaking, posterior to the attachment of the upper part of the scalenus medius. Between



the 4th and 5th and the 5th and 6th slips (numbered according to the vertebrae they arise from) the upper two roots of the long thoracic nerve (Bell) enter this surface. Below its lowest point of origin the muscle begins to stand away slightly from the vertebral column, and thus its medial surface comes into intimate contact with the first levator costae muscle, which is attached to the 7th transverse process: so the muscle can be said to be wrapped round the levator costae, which separates the lowest part of the medial surface (which is also the deepest) from Sibson's fascia covering the cervical dome of pleura. In other words the levator costae fills up the lowest part of the gutter. The marking for scalenus medius insertion on the first rib will therefore be in the form of a > with thick limbs enclosing the levator costae insertion. (The levator costae may be exposed by cutting through the posterior part of the scalene attachment to the first rib, just beyond the tubercle, and

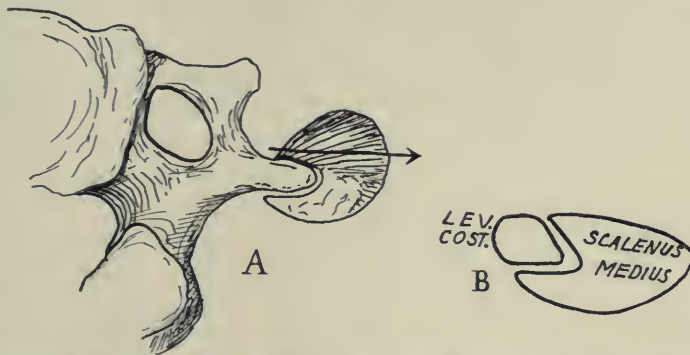


Fig. 1. A is a diagram to shew the relation of the scalenus medius to the transverse process. The arrow gives the general direction of the *r* nerve of Bell. B shews schematically the relations between the scalene and the levator costae; as they lie, for example, on the first rib.

reflecting it forwards so as to undo the fold in the muscle. The levator costae will be seen as a triangular muscular slip from the tip of the 7th transverse process to the first rib. Sometimes the fibres of the two muscles are partially intermixed but it is not uncommon to find that the scalenus medius is attached to the levator costae only by some loose connective tissue.)

The anterior surface is broad and flat. It looks forwards as well as slightly outwards and may therefore be called antero-external. The upper part, however, looks more directly forwards. The medial part of this surface lies behind the scalenus anticus: the brachial nerves intervening. The lateral part is partially under cover of the sternomastoid and, for the rest, in the floor of the posterior triangle: it is unnecessary to go into the details of its relations in these two areas. The roots of the long thoracic nerve appear on this surface. This surface is formed by the lower three slips of origin.

The posterior surface is applied to the levator anguli scapulae, the nerve to the rhomboids and posterior scapular artery passing downwards and backwards between the two muscles. This surface looks backwards as well as

outwards and so may be called postero-external. It is formed by the upper two slips of origin. This is narrow above but widens out below.

The lateral border is tendinous above but fleshy below.

Some of the fibres of the upper two slips (forming the posterior or postero-external surface) not uncommonly pass down to the second rib and thus form the scalenus posterior. In such a case the scalenus posterior arises from the second cervical vertebra and not the seventh as usually described in text-books. Hence this is a very long (but thin) muscle: which is of course merely a part of the medius.

This description explains how the roots of the long thoracic nerve pierce the muscle in order to appear in the floor of the posterior triangle. If the muscle were rising from the posterior tubercles, its plane would be behind the plane of the issuing nerves and it is difficult to understand how the roots pierce a structure on a posterior plane and still reappear on the same plane. But the origin above given, in conjunction with the thickness of the lower slips of origin, gives a surface for the roots to pierce.

## MISPLACED KIDNEY

BY PROFESSOR N. PAN,

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THE left kidney has been found in the lesser pelvis in a subject in the Dissecting Hall of the Medical College, Calcutta. Such low positions of the kidney are rare and hence I am publishing a short note of it.

The subject is an adult male. The left kidney is oval in shape. It is situated against the upper part of the left half of the pelvic surface of the sacrum. Its upper end lies against the anterior margin of the left ala of the sacrum. The lower end is lying on the piriformis against the greater sciatic notch. This kidney measures 3 ins. in length,  $1\frac{3}{4}$  ins. in breadth and  $1\frac{1}{4}$  ins. in thickness. On its anterior surface at the junction of the medial two-thirds with the lateral third there is a vertical groove, the upper half of which is shallow and lodges a renal vein running from the upper part of the hilum below to open into the terminal part of the left common iliac vein. The lower half of the vertical groove is very deep and represents the hilum. There are two renal arteries for this kidney. The upper one comes from behind the point of bifurcation of the abdominal aorta (*vide* fig. 1) and enters the upper end of the kidney at the upper part of the shallow groove. Its companion vein issues from the upper part of the hilum and runs along the shallow groove to the left common iliac vein as already mentioned. The lower renal artery comes from the left hypogastric artery and enters the hilum below and behind the ureter. Its companion vein opens into the left external iliac vein. The ureter leaves the hilum in front of the lower renal vessels and after a short course enters the bladder at the usual site. It is 6 ins. in length. This kidney is covered anteriorly by peritoneum and is surrounded by a scanty amount of areolar tissue. It is fixed in its position and not at all movable.

The tributaries of the left hypogastric vein corresponding to the branches of the anterior trunk of the left hypogastric artery unite into a trunk which crosses the pelvic surface of the sacrum to the right to open into the right hypogastric vein. The remaining tributaries of the left hypogastric vein unite into a trunk to join the left external iliac vein. The left suprarenal gland is normal in position and shape. The right kidney and suprarenal gland are in their normal position.

The caecum is situated in the right lumbar region one inch above the iliac crest. The loop of the sigmoid colon is very large and empty. It measures 15 ins. in length. The sigmoid mesocolon crosses the upper part of the 5th lumbar vertebra to the right iliac fossa and thence it crosses the brim of the lesser pelvis on the right side to terminate opposite the 3rd piece of the sacrum where the sigmoid colon is continued into the rectum.



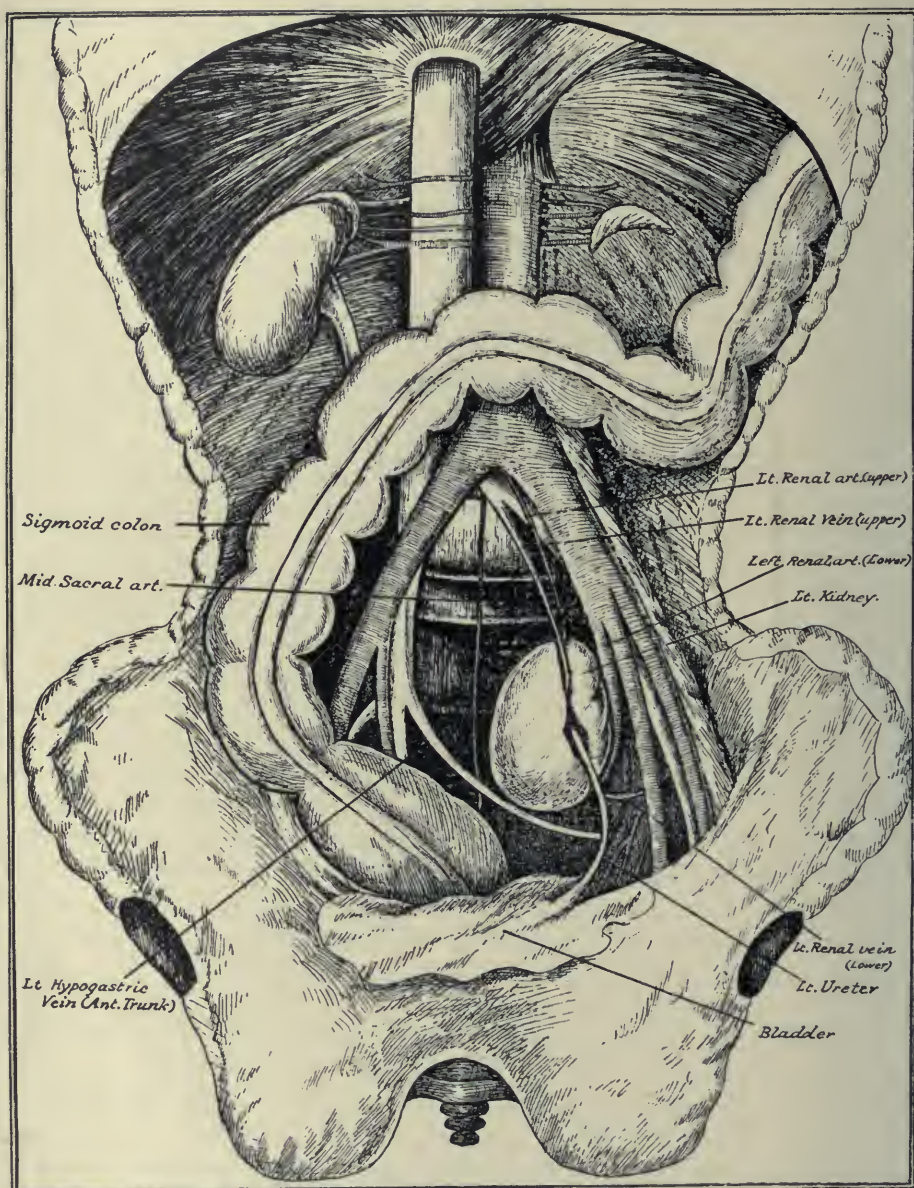


Fig. 1 Professor Pan's Case of Pelvic Kidney.

The left kidney in this case has got its arterial supply from the left hypogastric artery and the terminal part of the abdominal aorta. Thus the kidney has been developed in this unusually low place and has not migrated from its normal position after full development.

This unusually low position of the kidney is interesting from a clinical point of view as some of its pathological conditions are apt to mislead clinicians.

## A METHOD OF PREPARING BONES TO SHOW EPIPHYSEAL CENTRES OF OSSIFICATION

BY J. HAMILTON,

*Department of Anatomy, Queen's University of Belfast.*

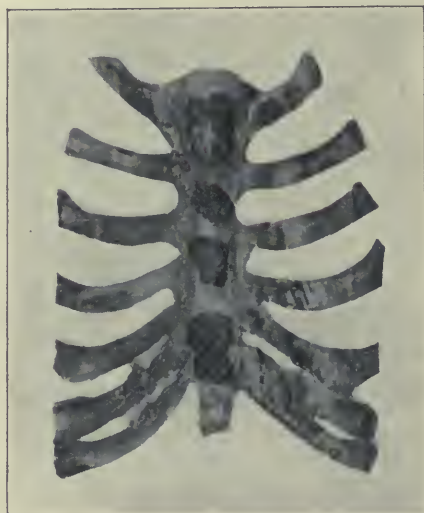
[The preparation of a permanent specimen to show the epiphyseal centres of ossification has been very successfully accomplished by the prosector in Anatomy at Queen's University, Belfast. His method, which is described below, is to make the cartilage transparent and slowly to saturate it with gum so that it retains its form and becomes perfectly hard. The specimens which have been prepared by him are permanent, some prepared twenty years ago are unchanged, and they are at least equal to those prepared by the Spalteholz method; they possess the advantage that they can be handled and closely examined by large numbers of students. In addition to the ossific centres I would add that the epiphyseal blood vessels are demonstrated better than in any other specimens I have seen, certainly much better than in Hunter's turpentine specimens. T.W.]

THE bones which I have used for preparation by this method were either (a) bones removed from fresh subjects or (b) bones removed from subjects preserved with formaline. In the fresh bones the centres of ossification are white in the finished specimen and in the formaline bones they are black; the difference seems to be due to the blood being retained in the latter. The bones must first of all be cleaned. Fresh bones are macerated in water in the usual way, care being taken that the bones are kept covered and the water frequently changed; otherwise I have found that the bones are liable to turn black. The macerating process must, of course, be controlled otherwise the epiphyses may fall off. Formaline bones do not require to be macerated since the periosteum can be stripped from them with forceps. The junction of the epiphysis with the shaft can be cleaned with fine scissors, but all cutting or tearing of the cartilage must be avoided for such injuries will appear in and blemish the finished specimen.

The cleaned bones must then be slowly dehydrated, beginning with a weak spirit and finishing with absolute alcohol; I allow 10 to 14 days for this process. The bones are then cleared in xylol till the cartilage is perfectly transparent but the process is stopped while the ossific centres are still opaque. This process I have found to take about 24 hours, but it requires to be carefully controlled since it is possible to clear macerated bones too much; the centres of bones preserved in formaline are dark in colour and remain visible even after long clearing. The bones are then to be embedded. The embedding substance which I have used is a mixture of gum mastic and gum sandarac dissolved as



far as they will dissolve in xylol. Either of the gums can be used separately or they can be mixed in any proportion, according to the colour which it is desired that the finished specimen should have; and the solution having been made it is filtered and allowed to evaporate to the consistency of thin cream. The specimen is allowed to remain in this solution for 6 to 8 weeks, and during this time slow evaporation must be allowed to take place until, at the end, the solution is so thick that it will hardly run off the specimen when it is lifted out. Care must be taken that the specimen is always kept covered with the solution.



The sternum of a child two years of age.

The drying of the bones requires the greatest care. They should be hung in a warm place free of dust. If too much of the embedding material clings to them it should be removed with a fine wooden probe; neither a knife nor a reagent must be used, for if the surface coating be damaged air will pass into the cartilage as the specimens are drying and produce white blotches which cannot be removed. The drying requires at least 3 or 4 months and in a large bone at least 6 months. At first the specimens must be examined almost every day, and if any part of the cartilage is drying more rapidly than the rest it must be brushed over very delicately with the embedding solution; and if the cartilage begins to have a "raw appearance" the surface coating is too thin and the specimen should be redipped in the solution. When the specimen is perfectly dry the bony part can be cleaned with fine glass-paper, and the whole specimen should then receive a coat of very thin solution of the gum applied with a fine camel-hair brush. The cartilage of a specimen prepared by this method should be perfectly transparent, and perfectly hard, and should be unaffected by exposure to the air.



## OBITUARY NOTICE

EMERITUS PROFESSOR JOHNSON SYMINGTON,  
M.D., F.R.C.S., LL.D., F.R.S.

DR JOHNSON SYMINGTON, Emeritus Professor of Anatomy in Queen's University, Belfast, died in Edinburgh on February 23rd, 1924. He had retired in 1918 because of severe illness, and in his retirement had enjoyed some measure of a return of the health which was characteristically his; yet, at the last, death came very suddenly to him, but came in a kindly way.

Johnson Symington was born in 1851. He had his early education at Taunton, and passed then to the University of Edinburgh, from which he graduated, with first class honours, in 1877. He commenced his life-long work at once, for in that year he became demonstrator under Turner in the Department of Anatomy at Edinburgh, with Cunningham as his senior colleague. He remained at the University only two years, for in 1879 he succeeded Dr J. Cossar Ewart as Lecturer in Anatomy at the School of Medicine, Minto House; but he must have learnt well the lesson Turner had to teach, and which he in turn so well taught to those who came to work with him, that it is to him who never spares himself that the keen zest of the search is given. He was called to the Chair of Anatomy in Belfast in 1893 as successor to Professor Peter Redfern, whom he was to succeed not only as a great teacher of Anatomy but as the greatest power of his day in the Belfast Medical School.

His life from the beginning was lived exceeding full. He obtained the diploma of M.R.C.S. (Eng.) in 1877, the F.R.C.S. (Edin.) in 1879, and proceeded M.D. in 1885, being awarded a gold medal for his thesis. In 1903 he was elected Fellow of the Royal Society and in 1915 Fellow of the Royal College of Surgeons of England; and in 1918 the honorary degree of LL.D. was conferred on him in Belfast. He was a life member of the British Association, and President of the Anthropological Section at Southport in 1903 and served as President of the Anatomical Society from 1904 to 1906; he was Vice-President of the Anatomical Section of the British Medical Association at the Edinburgh Meeting in 1898. He acted as examiner in Anatomy in the Universities of Edinburgh, London, Dublin, Glasgow and Manchester, and in Applied Anatomy and Physiology for the Indian Medical Service; and in the interests of the University of Belfast he expended his powers to the utmost. Shortly after his succession there, he was elected a member of the Senate and in 1901 he became Registrar, and with the inauguration of the new Queen's University of Belfast, under the Irish University Act of 1908, he was appointed one of the Commissioners to frame its statutes. His services were of the greatest importance in the difficult early days of the new University,

and his work of that time will long be remembered there. He was one of the honorary secretaries of the Better Equipment Fund; the new buildings of the University were very much in his care; and in 1916 he became the representative of the University on the General Medical Council. The University



EMERITUS PROFESSOR JOHNSON SYMINGTON,  
M.D., F.R.C.S., LL.D., F.R.S.

of Belfast has indeed good cause to revere the memory of the man who never spared himself in her interest.

Professor Symington was essentially a man of action. He was always a worker; what was most characteristic of him was his capacity to work, his untiring enthusiasm for his work, the pains he would take to demonstrate his observations to others, and the satisfaction he himself gained from his work. He was, too, a very direct worker; from first to last his papers are the

records of direct observations, and it need hardly be said that he was a keen observer. The whole trend of his researches was indicated well in the introductory address he gave to the class of Anatomy in Belfast University on October 31st, 1893. "I may perhaps be pardoned," he said, "if I consider the progress that has been made in our knowledge of the topographical anatomy of the human body, since this is a department with which my own researches have made me specially familiar." He was then, and he always was, a topographical anatomist, probably the greatest of his day. His first paper was "Notes of the dissection of a case of dislocation of the head of the right radius forwards" (*Journ. of Anat. and Physiol.* vol. XII), and his last "Endocranial casts and brain form; a criticism of some recent speculations" (*Journ. of Anat.* vol. I)—the very titles are typically his; and between these two he published in the *Journal of Anatomy* and in the *Journals* of the Edinburgh and Belfast Schools about sixty articles (see the bibliographical list attached to this article). His more important papers were on cranio-cerebral topography and on the form of the viscera; and on these subjects some of his descriptions will remain classical. His larger works were *The Anatomy of the Child*, *An Atlas of Topographical Anatomy*, *An Atlas of Skiagrams illustrating the Development of the Teeth*, and the volumes of *Quain's Anatomy* on *Splanchnology* and the *Nervous System* of which he was the editor.

His was indeed a forceful personality and in his vigour there may have appeared a *brusquerie*—a genial *brusquerie*—from time to time; yet it was easy to learn the simple straightness of all his work. He was exceedingly alert, and sometimes he may have seemed to be quick; but it was easy to admire the simple directness of what he did. He was of a direct and simple greatness; and it becomes easy for us to understand the depth of the affection he inspired in all who were his pupils or who worked with him.

The Symington Prize of the Anatomical Society carries his name; it is the name of one who was a great anatomist, a most capable administrator, and an upright man.

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## REVIEWS

*Körperbau und Menschwerdung. Konstruktionspläne, enthüllt durch eine Kausalanalyse der Menschlichen Beckenform.* By Dr. med. MAX VON ARX, Olten. Ernst Bircher: Leipzig.

Throughout a long gynaecological experience Dr. med. von Arx has interested himself in the mechanical aspects of biological problems. His attitude is attributed in part to the influence of his former teacher of anatomy, Prof. H. Meyer of Zürich, and, in addition, he has been brought by his profession into close contact with the practical mechanical problems of uterine prolapse and of pelvic deformities, from which he has been led to a study of the mechanism by which the normal shape of the human pelvis is attained. Considerable sections of the volume before us have been previously published in a series of papers to which references are provided.

In this work the author presents the data on which he relies in the elaboration of a method for the graphic representation of the pelvis. The method consists in the projection of selected points upon various planes, in a manner well-known in craniological studies; the pelvis is orientated according to the plan recommended by Meyer. Attention is drawn to some strikingly simple relationships found to exist between these points when studied in projection, a series of simple geometrical figures such as the hexagon and circle sufficing to describe their relative positions. The head of the femur is also shown to present interesting geometrical relationships to various parts of the pelvis.

The data provided relate to a single male and a single female pelvis, though we are assured—without presentation of the data—that a number of dimensions have been checked upon a “considerable number” of other pelves, whereby the author believes the “constancy” of certain proportions to be established. Such information is illustrative of the approximate nature of the investigation. The two pelves employed are stated to have been of “conventional” dimensions (though the male one is admittedly slightly asymmetrical); but the enquiry has clearly been too limited in scope and the measurements too rough to permit of any judgment of a particular pelvis as a representative one. This method of graphic representation may well turn out to have considerable value in facilitating comparisons of pelvic form at various ontogenetic stages, as well as for the study of inter-racial differences and for the comparative study of Primates. That the first of these has not already been carried out by the author is surprising inasmuch as a considerable part of the volume is devoted to a confident statement of the developmental mechanism of the human pelvis.

The author's conclusion, that the ontogenetic changes in shape of the human pelvis are “beyond doubt” due to the direct action of mechanical



force acting upon the skeletal tissues, is dependent on a number of assumptions which would have deserved more attention than has been given them. He argues that from a knowledge of the form of the adult pelvis one should be able to infer the mechanical forces which must have brought the embryonic pelvis to this condition. He naïvely assumes that ontogenetic changes are the result mainly or exclusively of gross mechanical forces, such as the hydrodynamic pressure of the visceral mass which is regarded as a predominating factor in human development; and further, that the nature of the effect on skeletal tissues of such a visceral pressure will consist in a yielding by reason of their softness. So long as no evidence is brought forward bearing on the validity of these assumptions, so long must the author's experiments with such materials as metal spheres and tubes, or with rubber bags remain totally irrelevant to the enquiry. Even the very points upon the pelvis selected for his geometrical construction fail to inspire confidence as likely to reveal the effects of visceral pressure upon the pelvis; a prominent place in the system is given to the upper margin of the *hiatus canalis sacralis*. Turning to a consideration of certain characteristic features which appear in the pelvis and vertebral column of the human embryo, it is said that the peculiar shape of the pregnant human uterus must be expected to lead to these very results. He supposes indeed, that the human embryo must be subjected to a "relatively increased pressure along its long-axis" because the human uterus is relatively shortened and of a more rounded shape than in other mammalia. We are informed, without evidence, that the "uteri of other animals do not exert so strong a longitudinally-directed pressure." Thus Dr. med. von Arx provides an extremely novel account of the physiological effects of phylogenetic changes of form, while he apparently even overlooks the mobility of the young embryo in the amniotic fluid.

It is nevertheless refreshing to meet with investigations in which the principal objective is the Interpretation of "Form" regarded as a part of the general problem of "Form and Function." Especially does the attitude adopted by the author of this work compare favourably with that of the writers (and they are not a few) who approach osteological problems as though a bone developed its characteristic form in splendid isolation, forgetful of the correlation undoubtedly existing between bones and the adjacent soft tissues in phylogeny as well as of their probable influence upon one another during the life of the individual. Though unfortunately Dr. med. von Arx has overlooked the relationship of pelvic form to muscles and other soft tissues external to the pelvis, yet he has very rightly included in his study of the pelvis a consideration of the relative position of the femur and lumbar vertebrae. In his enquiry into the process by which bones acquire their shape he has thus had a position of advantage over those who study single bones without consideration for other structures in the body of the individual. Yet it cannot be said that he has advanced our knowledge of this process. An extensive philosophy is combined with a paucity of data. The problem of "Form" is indeed one demanding

investigation by all available methods, including those of Experimental Anatomy; and there are, as this author has realised, many aspects of Medical Practice which claim for their understanding an earnest study of "Form and Function" with the attack directed towards the interpretation of Form.

A. B. A.

*Mechanism of the Brain and the Function of the Frontal Lobes.* By Professor LEONARDI BIANCHI. Authorised translation from the Italian by James H. MacDonald, M.B., Ch.B., F.R.F.P.S. (Glas.). With a foreword by C. Lloyd Morgan, LL.D., D.Sc., F.R.S. E. & S. Livingstone, pp. 348. £1. 1s.

The first part of this interesting and stimulating monograph is devoted to an account of the phylogeny, comparative anatomy and structure of the frontal lobe and also a résumé of the important experimental work conducted by the author over the long period of forty years. An excellent feature is the inclusion of a complete and critical survey of the literature bearing upon the widely discussed problem of the frontal area of the cortex and this makes the reader at once familiar with the history of this fascinating subject.

In the preface we are informed that the clinical aspect has been omitted since the author prefers to reserve this for separate and future publication. Although this omission has doubtless been necessitated by the wide range of treatment and consequent bulk of material, the inclusion of the clinical evidence would probably have removed a good deal of the hesitation which many readers will have in accepting some of the interpretations that are offered of the behaviour of animals after destruction of the frontal regions. Briefly, it was found that habitual actions or attitudes and the simpler forms of perception were practically unaffected by even extensive lesions of the frontal lobes, whereas faculties which had been acquired by education were grossly disturbed. These latter manifestations were only obvious after bilateral and extensive destruction. The movements of the eyes, pupils and ears obtained by electrical stimulation of certain parts of the frontal cortex are explained in an ingenious manner, it being stated that these cortical centres are connected with higher psychic processes and suggested that the movements are concerned with the mechanism of attention.

Histological investigations of the experimental material demonstrated connections between the frontal lobe and the head of the caudate nucleus, putamen, claustrum, the motor area and all the sensory fields of the cortex, but no direct connection with the optic thalamus was revealed. The reciprocal associations between the frontal and sensory areas leads the author to divide the cerebrum into frontal and post frontal regions, the former being correlated with a much superior order of consciousness than the latter and on this division he builds his psycho-neural thesis.

But the psycho-neural problem is a problem of unifying the two complementary but diverse aspects—psychological and neural—of one whole, and during the last half century three great minds, Huxley, William James and

Sir Charles Sherrington, have all arrived at the conclusion that the solution of the problem when it comes, will come from the side of psychology. A question of words arises here since Huxley and James used the term *metaphysics* and Sir Charles Sherrington uses the term *psychology*: but in view of James' statement that metaphysics is only "an unusually obstinate attempt to think clearly and consistently," we may regard modern psychology as a new science which in the last fifty years has grown up and become differentiated from within the ambit of metaphysics, and *for the particular purpose of this problem* we may use the terms as synonymous. From this point of view it seems to us that Professor Bianchi has placed himself among the group of people, to be found in all ages, whom Huxley in his day humorously referred to as "the noble untutored savages of common-sense": people who reject all metaphysical abstractions until they have become so far embodied in colloquial usage as to seem no longer metaphysical. "Consciousness," "the intellect," "cognitions," "the ego," "percepts," "judgments" and "psychic complexes" are among the metaphysical abstractions which go to make up the psychological half of Professor Bianchi's psycho-neural views; yet he tells us that "metaphysical abstraction...is insufficient to furnish us with elements that will serve as a key to positive cognitions" (p. 210). If this be so the problem will remain unsolved. To us James' contention of thirty years ago still holds good—"We seem, if we are to have an elementary psychophysics law at all, thrust right back on something like the mental-atom-theory, for the molecular fact being an element of the brain, would seem naturally to correspond, not to total thoughts, but to elements of thoughts."<sup>1</sup> We believe that modern psychology using the instrument of metaphysical abstraction will in due time provide us with such elements, and the problem will then be nearer its solution.

But, although Professor Bianchi has not solved the problem, it would be quite wrong to leave the impression that he has not made a large and important contribution to the data which will enter into its ultimate solution. We think that workers in this sphere of thought will come to the book again and again for the records of its author's long continued and laboriously careful experiments, for the wide range of its elaborately compiled data, and even for many of its conclusions. As we read and re-read what Professor Bianchi says on intelligence, on will, on inhibition and on instinct, we feel that he has brought us nearer to a solution of their nature. We heartily commend the book to all who are interested in the psycho-neural problem. In it they will find stimulus and help of the best kind, worthy indeed of the deservedly great reputation of its author.

Professor Lloyd-Morgan contributes a foreword emphasising the fact that the psycho-neural problem is here treated entirely as a subject of natural science.

Dr MacDonald is to be congratulated on the excellence of his translation.

<sup>1</sup> *Text-Book of Psychology*, p. 464.



*Hand Atlas of Human Anatomy.* By WERNER SPALTENHOLZ. Edited and translated from the 7th German edition by LEWELLYS F. BARKER.

The new English edition of Spalteholz's Atlas which has been translated by Professor Barker from the 7th German edition differs from the previous editions mainly in the addition of some new figures, especially those illustrating the development of bones. These latter have been taken from the marvellous preparations made by Spalteholz himself, some examples of which the Department of Anatomy at University College has been fortunate enough to obtain.

The present edition contains 994 illustrations, and is divided into three volumes. The work, by its title, indicates its position among anatomical works as, primarily, an atlas. A quantity of descriptive matter is, however, included, and since this is much more than is required for indicating the points and subject of each illustration and yet is far from being sufficiently detailed to serve as a general account of the anatomy of the human body, it would seem better to omit the greater portion of it entirely, or to amplify and incorporate it in separate volumes. Spalteholz, in his introduction to the 1st English edition, hints at the future possibility of the latter course.

It is difficult to find any but laudatory criticism to make on the beautiful illustrations which are so well known to English anatomists. Their clearness and accuracy and their artistic value are of the highest possible degree. Dealing with the anatomy of the right side of the human body, they depict every structure of gross anatomy and its relation to surrounding parts almost to perfection. One may point out little curiosities such as the pathological thyroid gland in Fig. 567, but such points calling for remark are difficult to find. The section on bones is supplemented by illustrated accounts of their development as noted above, and by admirably reproduced photographs of ground sections to illustrate the arrangement of the trabeculae. The diagrams showing muscular attachments to bones are perhaps the least satisfactory part of the work. In many cases, these appear to be very inaccurate, such, for instance, as the flexor longus hallucis or the fibula, and the obturator internus on the os innominatum.

The illustrations of muscles are less natural than the others, fidelity of reproduction being necessarily sacrificed in many cases for the sake of clarity. In the section on blood-vessels, the veins are depicted in an injected condition, a very obvious advantage. In the part dealing with the nervous system, the series of sections taken through the brain-stem are specially worthy of note. We can have little doubt that where atlases of human anatomy are in use, Spalteholz's work will hold one of the highest places. As a book for ready reference by those who have completed their anatomical studies, it will be of the utmost benefit to student and practitioner alike. As an aid to the student engaged in the study of anatomy it will also find its place, and we note that one text-book of practical anatomy gives marginal references to Spalteholz's atlas throughout the book by way of illustration. It is irrelevant, perhaps, to repeat here the frequently uttered warning that care be taken not to allow such an atlas to take the place of the human body for the student of anatomy.

## A COMPARATIVE STUDY OF THE FOOT AND TREAD INDEX

By GORDON HARROWER, M.B.

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IN the East, where the greater portion of the population are barefoot, opportunities for observing the different types of feet are more numerous than in the West. Having noticed a variation in the relative length of the second toe to the great toe, I was prompted to investigate whether the variation was constant in certain races or only an individual characteristic. Singapore offered an ideal field for the purpose as most of the races of the world are represented there. The method employed was simple; the apparatus consisted of a tin of black lead dusted on a flat board. The foot was pressed on the board and the subject then made to stand upright on a sheet of paper supporting his weight on one foot, the other foot just touching the ground. The outline so obtained was fixed later, by marking round with a pencil. It is a remarkable fact that while no difficulty was experienced in obtaining the native footprints, there was considerable trouble in obtaining the European prints, so much so, that the amount of explanation necessary to quieten the individual's suspicions of possible police interference, made the work so arduous that I have only a few European tracings, not sufficient to make a definite deduction therefrom. The results are somewhat statistical; at the same time I have worked out the tread index which may be obtained by dividing the maximum breadth of the footprint by the length from the tip of the impression produced by the second toe to the heel and multiplying by a hundred, thus giving an index figure which is not influenced by the actual size of the foot.

$$\text{Tread Index} = \frac{\text{Max. Breadth} \times 100}{\text{Max. Length}}.$$

In most books on artistic anatomy the second toe is shown slightly longer than the great toe, this condition being considered the ideal in Grecian art. According to Sir Wm. Flower, as quoted by Wood Jones, among hundreds of barefooted children in the highlands of Perthshire, Scotland, in no case did he find a second toe projecting beyond the great toe. Wood Jones, from his own observations, corroborates this for "Chinese coolies, Malays, Cingalese, and various inhabitants of India, Egypt, African races on the Nile, Madeira, Spain, Portugal and Italy." On the other hand, from my own observations among newly born babies at the Maternity and Free Maternity Hospitals, Singapore, I can affirm that in 71.9 per cent. out of a total number of 32 babies of mixed

nationality, the second toe is longer. Undoubtedly the little toe is undergoing phylogenetic reduction even in races which throughout life are barefoot, so that this characteristic is not artificial, due to boot-wearing. The reduction is very much greater in many animals as in the Bovidae, where the fifth metatarsal appears in the embryo but later disappears, and associated with its disappearance is the reduction of the fibula which can be traced in all stages throughout the animal kingdom. Among adults whom I have observed in connection with this work, I find that out of a total of 375 feet, 187 or 49.8 per cent. have the second toe longer than the great toe, the subjects being drawn from Tamils, Malays, Sikhs, Indians and Europeans. The relative lengths of the toes cannot be deduced from the footprints for the convexity on the under surface of the great toe is such that only the proximal portion of the terminal segment rests on the ground when standing erect, the toe thus appearing shorter than it really is. As the incidence of a longer second toe is greater among infants than adults, the inference is that the increase in the great toe is a physiological feature due to our mode of progression. This is more easily understood when we remember the imperfect condition of the skeletal elements of the foot at birth.

The great toe in all races is dominant, just as the third digit is dominant in the Perissodactyla. Our mode of progression makes it so, otherwise our lower limbs would on mechanical grounds require to be convex outwards as is the case in the Gorilla, or in the pathological condition of genu varum which is frequently associated with a high plantar arch tending to throw the weight on the lateral side of the foot. The same factor accounts for the rolling gait of the Simiidae while progressing in the erect attitude on the hinder extremities, as the body must be thrown over to one side to bring the centre of gravity of the body in line with the physiological axis of the foot.

The dominance is not due alone to the length of the great toe, as it is shorter than the corresponding digit of the gorilla, its relative length in man being due to reduction of the lateral digits. The dominance is also due to the great widening it has undergone in a transverse direction. I have only seen one case in which the third toe is longer than the second, and the second longer than the first, the digital formula being  $3 > 2 > 1 > 4 > 5$ . In the case which came under my observation, the subject was a Tamil, male, aged 30. He had been in the same employment for a considerable time, and to the best of my knowledge was strictly honest, although it is suggested that possessors of this type of foot are criminally inclined. Among the Primates, excepting Man, the third pedal digit or its representative is the longest. Of the skeletal material available at Raffles' Museum, Singapore, I find that in the Orang Utan (two adults and one young), *Hylobates* (one specimen), *Semnopithecus* (one specimen) the second metatarsal is the most projecting in the series, the third metatarsal being very little shorter, the metatarsal formula being  $2 > 3 > 4 > 5 > 1$ , a similar condition being found in the metacarpals, the elongation of the third digit of the foot being due chiefly to elongation of the proximal phalanx and





Fig. 1. Photograph of foot of male Tamil to show the long third toe.



Fig. 2. Note. Long third toe: the second and third metatarsals are considerably longer than the first. The fourth is longer than the first, a distinct Simian feature.

to a lesser degree of the second phalanx. In the *Macacus* (one specimen) and *Nasalis larvatus* (one specimen) the third metatarsal projected furthest in the series, in the *Nasalis* monkey distinctly so, but in the *Macacus* the difference was very slight. It was important to find out to which element of the pedal skeleton the elongation was due. I had X-ray photographs taken by Professor



Fig. 3. Note. Long great toe: the first three metatarsals have approximately the same degree of projection. The fourth metatarsal is shorter than the first.

Webster, Medical Electrician to the General Hospital, Singapore, to whom I tender my thanks. The photographs show that in the Tamil foot with elongated third toe the second and third metatarsals project equally; if anything, the third may project slightly less than the second yet considerably beyond the first metatarsal, corresponding very closely to the metatarsal condition in the Orang Utan, the metatarsal formula being  $2 > 3 > 4 > 1 > 5$ . The terminal phalanx of the third digit of the Tamil foot is slightly longer than that of the second (Fig. 2). For purposes of comparison in the human subject, I had

photographs taken of a European foot in which the great toe was considerably longer than the second (Fig. 3), digital formula  $1 > 2 > 3 > 4 > 5$ , and also of an Indian foot in which the second toe had a considerable degree of elongation (Fig. 4), digital formula  $2 > 1 > 3 > 4 > 5$ . In the European foot with large great toe the first three metatarsals have their distal ends projecting almost equally, metatarsal formula  $2 > 1 = 3 > 4 > 5$ ; in the Indian foot (Fig. 5) with long second toe the second metatarsal was considerably longer than the



Fig. 4. Photograph to show long second toe.

first and third, metatarsal formula  $2 > 3 > 1 > 4 > 5$ . The essential difference in these types of feet lies in the metatarsal series. The osseous skeleton of the great toe of the European foot is relatively and absolutely much heavier in structure than that in the other two types. Especially is this shown in the proximal phalanx.

The foot in which the third toe is longest is a retrogression towards a more primitive ancestor. The Gorilla, Chimpanzee, Orang Utan, and most of the Cercopithecidae have the third toe in advance of the others so that it is a distinctly Simian type of foot. Not only does this particular type of human



foot agree with the Simian type in superficial appearance but also in the osseous skeleton of its metatarsals with the exception of the hallux as I have shown. It is a very uncommon type in Man for, although I have watched the barefooted pedestrians of Singapore for many hours, I have not seen another case. In the Simiidae, however, the interosseous muscles are grouped about the third toe as axis (although some Gorillas have the human arrangement). It is not possible to say with certainty whether the interossei in the case of the Tamil mentioned were grouped around the second or third toe as his command of individual movement of the toes was limited. The type of foot with the longer second toe is nearer the Simian type than that with the elongated great toe as the metatarsal formula also agrees though not so closely with the Simian metatarsal formula. We may regard the type of foot with the elongated great toe as highest in the evolutionary scale and therefore the great toe is undergoing a progressive increase. The great toe has an element less in its constitution than the remaining toes. It has long been a matter of doubt whether the so-called metatarsal is really a metatarsal or phalanx. As the three types of foot show, there is a progressive tendency to reduction of the metatarsals and an increase in the phalangeal elements of the great toe. The ossification of the first metatarsal corresponds with the ossification of a phalanx<sup>1</sup>. All these facts lend support to the view that the metatarsal is missing and not the phalanx.

It is interesting to note that in the individual possessing the foot of the highest type with the elongated great toe, the left upper lateral incisor was not developed, the left upper canine being modified in the direction of an incisor, its lower margin not projecting below the free dental margin as in normal canines. Also the third upper and lower molar teeth never erupted, although the individual was long past the age when they usually erupt. These dental facts represent an advance in the evolutionary march compared to the condition in the ancient Incas in whom four molar teeth frequently developed. There is apparently no racial distinction to be drawn from the relative lengths of the great and second toes, although the greatest degree of dominance of the great toe is probably to be found among European races. Throughout the Primates I have mentioned, except Man, the base of the second metatarsal is notched similar to the base of the second metacarpal, the joint being mechanically similar to the second metacarpo-carpal articulation.

The tread indices obtained from the footprints are rather remarkable. Obviously a certain amount of variation is to be expected, yet the index figures range from 34 to 43. A maximum variation of 9 for all races examined—European and Asiatic. These figures are more remarkable when one considers that the absolute difference is multiplied by 100 when working out the indices. Each race shows a certain degree of constancy. Among the Chinese, 69 out of 122 feet fall into the group 38.1 to 41.0, or 56.55 per cent. of the total. The Sikhs and Indians other than Tamils have each the same group incidence,

<sup>1</sup> Admittedly the first metatarsal occasionally ossifies from three centres.

36.1 to 39.0, a percentage of 64.58 for Sikhs and 55.32 for Indians. The Sikhs are a tall, heavily built race with large feet, yet their tread index is considerably below that of the Chinese. The Tamils have the lowest index of all



Fig. 5. Note. Long second toe. The second metatarsal is much longer than the first, the third, although longer than the first metatarsal, is much shorter than the second. The fourth is shorter than the first. (Unfortunately the toes were not extended when the plate was taken.)

the races falling into the group 35.1 to 38.0 with a total of 54 out of 102 feet, or 52.94 per cent. Malays and Europeans have the same group incidence, namely 37.1 to 40.0, giving a percentage of 63.89 for Malays, but as I have already indicated, the number of Europeans observed is too small to make a

definite statement. The outline of the foot has a certain amount of interest, at least among the Asiatic group who are mostly unbooted. It is undeniable that the outline is considerably modified in the booted races. In the three Pangan Semangs quoted by Duckworth, there appears a tendency to inversion



Fig. 6. Tracing of a footprint of a Tamil male aged 25 years. This shows a more exaggerated degree of inversion of the great toe and eversion of the lateral four toes. While quite a common type of Tamil footprint it does not occur so frequently as Fig. 7.

Fig. 7. Tracing of a footprint of a Tamil male aged 30 years to show the inversion of the great toe. This represents the average type of Tamil footprint.

of the great toe. This is particularly marked in two, but in the third case is not so obvious. Among the Tamil population of Singapore there is a similar tendency, the great toe turning inwards, the lateral four toes being spread out so that a distinct interval intervenes between the great toe and the second



toe ranging up to as much as 2 cms. This condition is beautifully illustrated in the copy of the footprint of a Tamil male aged 25 shown in Fig. 6. While it is comparatively common to find as wide a divergence of the great and second toes, as is shown here, it is more common to find the interval slightly reduced as depicted in Fig. 7. From comparison with the Primates, which retain a well developed hallux, this is the condition one would expect in races which do not wear foot protection. It is also seen in the newly born child when the foot is at rest.

The Chinese wear wooden soles with a strap over the toes along the line of the metatarsals and therefore the toes tend to be closer together. The Sikhs wear a wooden sole with a peg projecting upwards which is retained between the great and second toes so that these toes incline toward one another due to the muscular action involved. The footprint of the Sikh frequently shows a distinct circular area in the position of the peg due to the pressure, this area not being in contact with the sole. Many Sikhs, of course, wear soles like those described for Chinese. Tamils seldom wear any form of foot protector. Among the better class Asiatics the ordinary leather shoe is worn.

Foot deformities are comparatively rare among the natives.

Dr Smith had a case of congenital hallux valgus of which I saw the X-ray plate. The patient had never worn any foot protector. Out of the total number of 355 Asiatic feet observed, 6 showed the condition of pes cavus and 25 that of flat foot. I have not seen a case of rhachitis among the native population of Singapore.

I append the actual measurements of the feet.

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*Actual Measurements of Feet.*

Abbreviations: Ham. Toe = Hammer Toe.

P.C. = Pes Cavus.

## Tamil I.

	Length of tread		Breadth of tread		Tread index		2nd toe longer		Interval between 1st and 2nd toes		Flat foot	
	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.
Tamil	20.4	20.5	8.4	8.2	41.18	39.99	+	+	1.4	1.3	-	+
"	25.5	25.5	8.8	9	34.51	35.30	+	-	1	.8	-	-
"	20.5	21	7.5	7.7	36.76	36.67	-	-	1.3	1	-	-
"	21.7	21.8	9	8.8	41.47	40.36	-	-	.8	.9	-	-
"	22.4		9		40.18		=		1.2		-	
"	22.9	22.8	8.4	8.4	36.68	36.84	+	+	1.3	1.2	-	-
"	22.3	22.5	8.5	8.5	38.12	37.78	+	+	1.3	1.2	-	-
"	22.4	23	8.2	8.5	36.61	36.96	-	+	1	.9	+	-
"	27	26	10	9.5	37.03	36.54	+	+	1.2	1.4	-	-
"	21.2	21.2	9	9	42.45	42.45	+	+	2.2	2.2	-	-
"	23.2	23.5	8.8	9.2	37.93	39.14	+	+	2.2	1.5	-	-
"	24.6	25.4	9.5	9.8	38.62	38.59	+	+	2.3	2.4	-	-
"	22.4	21.8	8.7	8	38.85	36.69	+	+	1.3	.4	-	-
"	23	23	8.2	8	35.66	34.78	+	+	.4	.5	-	-
"	23	23.2	8.4	8.2	36.53	35.34	+	+	1.1	1	-	-
"	23.4	23.3	8.7	8.5	37.18	36.48	=	=	.9	.7	-	-
"	24	23.8	9	9.2	37.50	38.66	=	=	1.8	1.7	-	-
"	21.2	21.2	8	8	37.74	37.74	-	=	1.4	1.6	-	-
"	21.9	22.5	7.7	7.8	35.17	34.66	+	+	1.1	1.5	-	-
"	21.8	21.8	8	8	36.69	36.69	-	-	1	1.5	+	+
"	24.1	24.2	8.3	9	34.44	37.18	+	=	1.4	1.1	-	-
"	23.7	23.2	8.4	9	35.45	38.79	+	+	1.2	.7	-	-
"	24.2	24.5	8.5	8.3	35.13	33.88	+	+	2.2	2	-	-
"	23.6	23	8	7.8	33.90	33.91	+	+	1	.5	-	-
"	24	24	9.5	9	39.59	37.67	-	-	1.3	1.5	-	-
"	24.7	24.6	10	10	40.49	40.65	+	+	1.3	1.2	+	+
"	22.6	23.4	8	8	35.40	33.88	-	+	1.7	2	-	-
"	23.4	22.5	8.2	8.5	35.05	37.78	+	=	.9	.8	-	-
"	23.1	23.4	7.7	7.8	33.34	33.34	+	+	.4	.4	-	-
"	23.3	23.5	8.7	8.6	37.34	36.59	+	+	1.5	1.4	-	-

## Tamil II.

Tamil	21.3	21.7	7.5	8	35.22	36.86	+	+	.4	.7	-	-
"	23.6	23.9	8.6	8.5	36.44	35.56	-	-	.7	.5	-	-
"	23.6	23.8	8.7	8.8	36.86	36.98	-	+	.8	.8	-	-
"	22.8	23	8.5	8.7	37.28	37.83	+	+	.8	.7	-	-
"	24	24.3	8.5	8.5	35.42	34.97	+	+	2.4	2.3	-	-
"		22		8.5		38.64		-		1	-	-
"	21.2	21.8	7.8	8	36.80	36.69	=	=	.7	1.3	-	-
"	24.4	24.4	8.7	8.8	35.66	36.07	+	+	1.7	1.8	-	-
"	24.3	23.9	9.3	9	38.27	37.65	+	+	.4	.6	-	-
"	24.8	24.8	8.8	8.6	35.48	34.67	+	+	2.8	2.1	-	-
"	22	22.2	9.1	9.2	41.36	41.44	+	+	1.2	1.7	-	-
"	23.7	23.7	9.8	9.8	41.35	41.35	+	+	1.5	1.1	-	-
"	22.9	22.6	9	9.1	39.30	40.18	+	+	1.7	1.8	-	-
"	22.7	22.7	8.5	8.2	37.44	36.13	-	-	1.4	1.2	-	-
"	23	22.8	9	9	39.13	39.48	-	-	1.7	.7	-	-
"	24	23.8	8.6	8.4	35.83	35.30	-	-	1.3	1.9	-	-
"	22.8	22.1	8.5	8.2	37.28	37.10	+	+	1	2	-	-
"	23.1	23.5	9	9	38.95	38.29	-	-	1	1	-	-
"	22	22.2	7.8	7.7	35.46	34.68	+	+	1.7	1.4	-	-
"	24.4	24.3	9.8	10	40.16	41.15	+	+	1.7	1.8	-	-
"	23.2	23.2	9	9	38.79	38.79	+	-	.8	1.1	-	-
"	24	24	9.5	9.7	39.59	40.42	-	-	1	.8	-	-

## Chinese I.

	Length of tread		Breadth of tread		Tread index		2nd toe longer		Interval between 1st and 2nd toes		Flat foot	
	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.
Hylam	23.7	24.3	9.5	9.5	40.09	39.09	=	=	1.8	1.5	-	-
Teochow	24.6	24.6	9	9	36.59	36.59	+	+	.7	1.0	-	-
Hokien	23.8	24.2	9.4	9.6	39.50	39.68	+	+	.6	.9	-	-
"	24	23.6	9.2	9	38.33	38.16	+	+	1.1	.9	-	-
"	23.5	24	8.3	8.7	34.51	36.24	=	=	.4	.4	-	-
"	23	22.7	9	9	39.13	39.74	+	+	.9	.6	-	-
"	23.8	23.2	8.8	9	36.98	38.79	+	+	.5	.3	-	-
Teochow	22.8	22.8	8.5	8.4	37.28	36.84	+	+	1.3	1	-	-
Hylam	23	23	8.9	8.6	38.70	37.40	+	+	1.0	.8	-	-
Teochow	25.2	25.5	8.2	8	32.54	31.37	+	+	1.2	1.0	-	-
Hylam		22.5		8.7		38.67		=		.7		-
Hokien	22.6	23	9	8.8	39.82	38.23	+	+	.5	.4	-	-
"	22.4	22.8	8	8	35.72	35.10	+	+	.8	.8	P.C.	P.C.
Hylam	23.2		9.5		40.95		-		.6		-	-
"	24	23.6	9	9.5	37.50	40.25	=	+	.6	.4	+	+
Hokien	23.8	22.4	8.7	9	36.56	40.18	=	=	.2	.5	-	-
Hylam	23.4	22.3	8.1	8	34.63	35.88	+	+	.2	.4	-	-
Hokchia		23.5		8.8		37.44		=		.1		-
Hokien	22	22.5	7	9	32.82	40.01	=	=	.5	.3	-	-
"	22	22	8	8	36.37	36.37	=	=	.7	.7	-	-
"	23.2	23.7	8.2	8.3	35.34	35.02	+	+	.7	.4	-	-
Hokchia	21.7	21.8	8.5	8.6	39.16	39.45	+	+	.6	.8	-	-
Hokien F.	19.7	18.9	8	8	40.61	42.33	+	+	1	1.7	+	+
Foochoo F.	17.6	17.7	7	6.8	39.77	38.41	=	=	.6	.7	-	-
Hokien F.	19.4	19.6	8.1	8.1	41.76	41.32	=	=	.4	.3	-	-
Macao F.	19.8	19.8	7.8	8.1	39.40	40.91	+	=	1.2	1	-	-
Cantonese	22.2		9.8		44.14		=		1.5		-	-
Hokien	24	24	9.8	10	40.83	41.67	=	=	1	.5	-	-
Teochow	24.5	24.3	9.8	9.6	39.99	39.51	+	+	1	.5	-	-
"	23.4	23.2	8.8	9	37.61	38.79	+	+	.2	.3	-	-

## Chinese II.

Hoofoo	24.1	24.1	10.1	9.5	41.90	39.42	=	=	1.4	1.4	-	-
Hokien		24		9.2		38.33		-		.4		-
"		24.3		9.4		38.68		+		1.4		-
"		23.4	10		42.74		+		.8		-	-
Hokchia	23.8	23.9	9.6	9.5	40.33	39.75	=	+	.6	.4	-	-
Teochow	22.8	22.6	9.3	9	40.80	39.82	=	=	.6	.4	-	-
Hokien	24	23.8	9.2	8.6	38.33	36.13	=	=	1.1	1	-	-
"	24.2	24.4	9.7	10	40.09	40.99	=	=	1	.6	-	-
"	22.6	23.2	9.6	9.8	42.48	41.17	=	=	.4	.8	-	-
"	24	23.7	9.5	9.3	39.59	39.25	+	+	.8	1	-	-
"	21	21	8.3	8.2	39.53	39.04	+	+	1	1	-	-
"		23.5		9.5	40.42		=	=		.8		-
"	22.4	22.9	9	9.5	40.18	41.49	=	=	1.2	1.3	-	-
"	22.7	22.8	9	8.8	39.65	38.60	=	=	.7	.8	-	-
Hokchia	22.6	22.8	8.8	8.8	38.94	38.60	+	+	.4	.5	-	-
Hokien	21.8	21.6	9	8.7	41.28	40.27	+	+	.5	.7	-	-
Teochow	24	24	9.2	8.8	38.30	36.67	+	+	1	1.2	-	-
Hokien	23	23	9.3	9.5	40.43	41.30	=	=	.5	.2	-	-
Hylam	23.8	23.8	9.1	9.3	38.23	39.07	+	+	1	.9	-	-
Hokien	23	23	8.1	8	35.22	34.78	=	+	.3	.4	-	-
"	21.8	21.7	8.7	8.5	39.90	39.16	=	=	.8	.6	-	-
Hylam	22.4	22.7	8.3	9	37.06	39.65	=	+		.6	-	-
Hokien	24	24	10	9.8	41.67	40.83	-	=	1	1	-	-
"	20.4	20.5	8.2	8.3	41.18	40.49	=	+	.4	.8	-	-
Hingwah	22	22	8.2	8.2	37.27	37.27	=	=	1	.6	-	-
Teochow	23.8	23.2	9.5	9.8	39.91	42.23	=	+	.9	.6	-	-
Kheh	23.3	23.3	8.8	8.8	37.77	37.77	+	+	.5	.6	-	-
Teochow	22.4	22.4	8.7	8.1	38.85	36.18	=	+	.5	1	P.C.	P.C.
"	24.2	24.3	9.5	9.5	39.17	38.99	+	+	.5	.6	-	-
Hylam	24.3	24.3	9.5	9.4	38.99	38.67	+	+	.8	1	-	-
Hokien	22.5	22.8	9	9	39.99	39.48	+	+	.8	.8	-	-



## Chinese III.

	Length of tread		Breadth of tread		Tread index		2nd toe longer		Interval between 1st and 2nd toes		Flat foot	
	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.
Hylam	22.5	22.5	8.8	9	39.11	41.88	+	+	.3	.4	-	-
Hochchew	22.8	22.8	9.5	9.6	41.67	42.11	-	-	.4	.2	-	-
Hokien	22.7	22.7	9.3	9.3	40.98	40.98	-	-	1.4	.9	+	+
Kheh	23.5	23.3	8.8	8.8	37.44	37.77	-	-	.5	.5	-	-

## European.

English	23.6	23.4	9	9	38.14	38.46	-	-	1.1	.7	-	-
"	24	24.4	8.7	8.7	36.24	35.66	-	-	.4	.5	-	+
"	24.8	25	8.8	9	35.48	35.99	=	-	1	.7	+	+
Dutch	24.3	24.2	9.2	9	37.86	37.18	-	-	.9	.9	-	-
French	25.6	25.5	10.2	10	39.85	39.22	-	-	.2	.2	-	-
English	24.1	24.1	9.5	9.5	39.78	39.78	+	+	1.4	1	+	+
"	25.6	25.1	9.3	9.1	36.34	36.24	+	+	.5	.5	-	-
"	25.8	26.2	9.6	9.6	37.21	36.64	+	+	.8	.7	-	-
Dutch	23.2	23.6	8.7	9	37.50	38.14	-	-	.8	1	-	-
English	25.3	25.8	10	10.5	39.53	40.70	-	-	.5	.4	+	+

## Malay and Javanese.

Malay	22.9	23.3	8	8	34.93	34.34	-	-	.3	.4	-	-
"	22.9	23	9	9	39.30	39.13	-	-	1.3	1	-	-
"	25	25.3	9	9.3	35.99	36.76	+	+	1	1	-	-
"	23	23.3	9.5	9.7	41.30	41.63	+	+	1.7	1.8	-	-
"	23.2	22.6	8.6	7.6	37.07	33.62	+	+	.9	.7	-	-
"	21.8	21.3	8.3	8.1	38.07	38.03	-	-	.9	1.4	-	-
"	24.6	24.8	9.5	9.8	38.62	39.51	+	+	.3	.5	-	-
Javanese	22.3	22	8.7	8.6	39.01	39.09	=	=	.3	.8	-	-
Malay	26.3	26.2	10.1	9.9	38.40	37.79	-	-	.6	.4	-	-
"	21.5	21.4	8.5	8.3	39.54	38.80	-	-	1	1.5	-	-
"	22.4	22.3	8.4	8.5	37.51	38.12	+	+	1	1.6	-	-
Javanese	23.6	23.3	9.5	9.5	40.15	40.77	+	-	.8	.7	+	+
Malay	22.8		9.4		41.23		-		.6		-	
"	26		9.3		35.77		+		.2		-	
"	23	23.2	9.2	8.8	39.83	37.93	-	-	.5	.3	-	
"	21	21	7.5	8	35.71	38.19	=	=	.5	1.2	-	-
"	23.4	23.8	9	9.3	38.47	39.07	+	+	1.3	1	-	-
"	22.7	23	8.7	8.5	38.32	36.96	=	=	.4	.4	-	-
"	24.7	24.8	9.5	9.5	38.46	38.30	+	+	.7	1.1	-	-

Sikh.

	Length of tread		Breadth of tread		Tread index		2nd toe longer		Interval between 1st and 2nd toes		Flat foot	
	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.
Sikh	26.3	26.3	9.7	9.7	36.81	36.81	=	+	1.4	1.9	-	-
"	24.8	24.6	9.4	9.4	37.89	38.21	=	=	.9	.7	-	-
"	24.5	25.2	9	8.5	36.73	33.73	=	+	.8	1	-	-
"	27.2	26.9	10.2	10.1	37.50	37.54	+	+	1.5	1.5	-	-
"	26.8	27	10	9.8	37.32	36.29	=	=	1.5	1.5	-	-
"	25.4	25.7	9.5	9.5	37.41	36.97	+	+	1.6	1.4	-	-
"	26.2	26	9.3	9.4	37.17	36.15	=	=	.8	1.3	-	-
"	23.3	23.7	8.8	9	37.77	37.93	=	=	1.5	1.5	-	-
"	24.4	25.6	9.5	9	38.93	35.16	=	=	1.3	1.5	-	-
"	25.7	25.6	10	9.7	38.91	37.89	-	-	1.5	.6	-	-
"	25.7	26.2	9.5	9.7	36.97	37.02	=	=	1.5	1	-	-
"	25.6	25.7	9.8	9.3	38.28	36.19	=	=	1.5	1.3	-	-
"	26.4	26.4	10.3	10.3	39.01	39.01	+	+	.7	.7	-	-
"	25.5	25.8	9.7	10	38.05	39.22	-	-	.5	.9	-	-
"	23.2	23.5	9.2	9	39.66	38.29	=	=	1.1	1.5	-	-
"	23.4	23.8	9	9.3	38.46	36.48	+	+	1.5	1.5	-	-
"	25.3	25.5	9	9	35.57	35.30	+	+	1.1	.5	-	-
"	23	23.3	9.5	9.3	41.30	39.91	=	=	.3	.8	+	+
"	25	25.2	9.8	9.2	39.20	36.51	+	+	1.2	.8	-	-
"	26.2	26.3	10.5	10.4	40.07	39.54	-	-	1.5	1.8	-	-
"	28.5	28.3	10.6	10.4	37.18	36.75	+	+	.8	1	-	-
"	24.5	24.4	9.7	9.8	39.59	40.16	=	=	1	1.8	-	-
"	24.5	24.2	10.3	10.3	42.04	42.56	=	=	.7	.7	-	-
"	24.5	24.4	9	9	36.73	36.88	+	+	.7	.7	-	-

Indian.

	Length of tread		Breadth of tread		Tread index		2nd toe longer		Interval between 1st and 2nd toes		Flat foot	
	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.
Malabari	24.3	24.1	9.2	9	37.86	37.35	+	+	.3	.7	-	-
Indian	22.5	23	9	9.5	39.99	41.30	-	-	1	.8	P.C.	P.C.
Malabari	22.5	22.4	8.5	8.5	37.78	37.95	+	+	1.3	1.5	-	-
"	23.2	23.7	9.5	9.5	40.96	40.09	=	=	2	2	-	-
Gurkha	22.2	22.6	8.3	8.8	37.39	39.94	=	=	.3	.6	+	+
Pathan	24	24.7	9.2	8.8	38.32	35.63	-	-	.6	1	-	-
"	23.5	23.6	9.2	9.6	39.14	40.68	+	+	.2	.5	-	-
"	23.4	23.8	8	7.8	34.19	32.77	+	+	.5	.6	-	-
Indian	24.7	24.8	9	9.4	36.43	37.89	+	+	1	.8	+	+
"	23.4	23.4	9.7	9.5	41.46	40.60	-	-	1.5	1	+	+
"	22.3	23	8.8	8.7	40.00	37.83	+	+	.5	.9	-	-
"	24	23.8	9.5	9.2	39.59	38.66	-	-	1	.7	-	-
"	22.2	22.7	8.5	8.8	38.28	38.77	-	-	.8	.3	-	-
"	24.4	24.7	9	9	36.88	36.43	+	+	.5	.4	-	-
"	25.7	25.3	9.8	10	38.15	39.53	+	+	1	.7	+	+
"	23.6	23.7	10	10	42.37	42.20	=	=	1	.4	-	-
"	25	25.4	9.3	9	37.20	35.43	+	+	.2	.2	-	-
"	23.5	23.2	8.3	8	35.32	35.78	=	=	.7	.8	-	-
"	22	23	8	9	36.37	39.13	-	-	.7	.7	-	-
Goanese	23	23.3	8.3	8.4	36.09	36.04	=	=	.7	1	-	-
Indian	24.7	24.2	8.4	8.8	34.01	36.37	=	=	.7	.7	-	-
"	22	21.8	8.1	8.1	36.82	37.15	=	=	2.5	2.3	-	-
"	22.6	22.6	8.8	8.6	38.94	38.06	-	-	1.6	1.3	+	+
"		24.5		9.5		38.77		+		.4		-
"	23.5	23.6	8.8	8.5	37.44	36.02	=	=	.4	.7	-	-
"	22.5		8.7		38.67		-		.7		-	-

Table of Tread Indices indicating the Predominant Groupings.

	Under 34										Over 43										
	34.1-35		35.1-36		36.1-37		37.1-38		38.1-39		39.1-40		40.1-41		41.1-42		42.1-43		Total		
	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.	R.	L.			
Chinese	3	2c	1c	3c	3c	4c	7c	7	5	8	12	15	14	11	9	6	6	2	3	1	122
Tamil	2	4	2	5	12	4	8	13	9	8	6	4	3	3	4	4	3	1	1	—	102
Sikh	1	—	—	1	2	4	9	7	4	5	2	4	4	1	1	1	—	2	—	—	48
Malay	1	1	1	3	0	0	2	2	2	6	5	4	4	1	1	2	1	—	—	—	36
Indian	1	2	0	1	3	5	3	4	5	4	5	3	2	2	3	1	1	1	1	—	47
European	—	—	—	1	2	2	2	3	1	1	2	3	2	—	1	—	—	—	—	—	20



## THE SACRO-ILIAC JOINT

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THE following observations are based on the study, extending over a period of three years, of two hundred sacro-iliac joints, both male and female, of all ages, obtained from dissecting room and post mortem subjects.

### 1. *The Influence of Age and Sex on the Mobility of the Joint.*

Zaglas as early as 1851, and Duncan in 1854, described a normal rotatory movement at the sacro-iliac joint; but later on Quain, and other observers, laid stress on the presence of transverse strands of fibrous tissue bridging across the joint, and connecting one articular surface to the other; hence the articulation became regarded as of the amphi-arthro-dial type. More recently, however, Nuttall pointed out that, even when this condition was present, slight movement could often be obtained. The present series show that in males of late middle and advanced age the joints *are* usually amphi-arthro-dial; in many cases complete ankylosis is present; but the number forms much too small a percentage of the whole to form the basis of a description of the normal state of affairs. In fact there is every reason to believe that such joints are not normal at all, but the result of senile pathological changes.

The estimation of the degree of movement present at these articulations is a matter of considerable difficulty, but an attempt has been made to classify them according to mobility.

During the first twelve to fourteen years of life it is almost impossible to draw any distinction between the joints of the two sexes (36 were examined); but, with the advent of puberty, marked secondary sexual differences make their appearance. Those of the *male* progress along lines of strength and security, that is to say, the ligaments thicken and become stronger, to meet no doubt the increased strain involved in the harder physical tasks which fall to man's lot. Mobility in other words is sacrificed for strength. In the *female*, on the other hand, the reverse condition is seen. Here strength and solidity are sacrificed in favour of increased mobility; the ligaments and soft parts of the joint remaining comparatively lax; an adaptation again, as in the male, to function, the important female function of parturition.

Fig. 1 shows that there is a diminution of movement in both sexes from birth up to puberty, then in the female a rapid increase takes place up to the age of twenty-five years, when the maximum degree of movement is attained. The dotted curves represent the average age incidence of some of the sacro-

iliac diseases such as tuberculosis, infective arthritis, sprains, etc. as determined by the examination of a small number only, viz. two hundred and fifty cases from the Guy's Hospital reports. It will be noticed that the maximum age incidence of tuberculosis infection falls between the years of twenty to twenty-five, and this corresponds with Porrier's observations.

That of the other affections is very similar. As would be expected, sacro-iliac disease occurs by far the more commonly in the female sex and to the greatest degree—as the curves show—at a period when the joints are most movable.

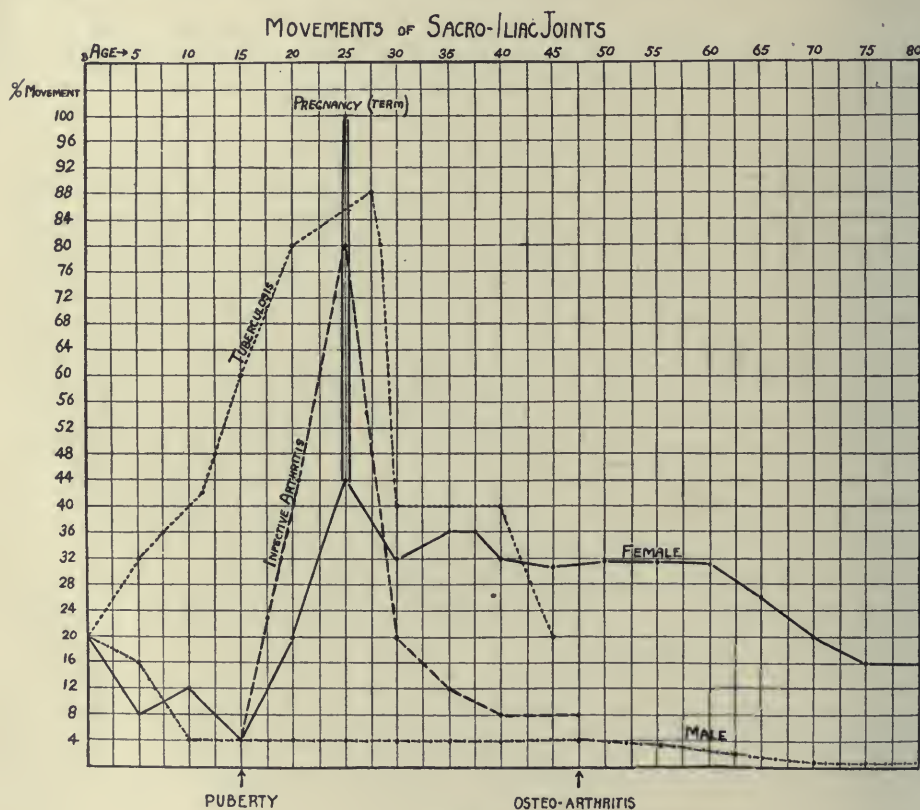


Fig. 1.

It is seen that in the case of the *female* there is a gradual diminution of movement from the age of twenty-five to the age of fifty years, after which it becomes more rapid; but even in advanced age some mobility persists.

## 2. A Comparison of the Mobility and Function of the Joint in the two sexes.

In the case of the *male* the degree of movement is slight in amount up to the fiftieth year, becoming progressively less and less after this until finally the joint becomes usually completely ankylosed.

It was found that 37 per cent. of the total number of male joints of all ages examined, 105 in number, were completely immovable and ankylosed. *The greater the age of the subjects, the higher was the proportion of immobile joints.* Thus the proportion of ankylosed joints in subjects above fifty years of age was 76 per cent., and not a single example was obtained under the age of fifty years. Forty-four joints from subjects all over fifty years of age were examined.

From this series it seems that ankylosis of the joint in advanced age is confined strictly to the male sex. It was not present in any of the 105 female specimens examined.



Fig. 2. Intra-Articular Tubercle on Sacral Surface.

Derry has shown that the joint stability is increased by interlocking of rough prominences and depressions situated in the ligamentous post auricular area of the joint. In addition to this it was found that if the sacral surface of the articulation itself is examined, at the junction of the two limbs, towards the anterior margin of the joint, a small tubercle, or eminence, covered by cartilage, can often be seen interlocking with a corresponding depression on the auricular surface of the ilium (Fig. 2). Unlike the tubercle described by Derry, which is extra articular in position, this one is situated within the joint cavity itself. It was present in 88 per cent. of the 55 male cases examined, well



marked in 75 per cent. of these cases, not so well defined in the remaining 25 per cent. Although not strictly speaking a male characteristic, in only 15 per cent. of 95 female cases examined was there any corresponding elevation, and it was never well defined. It is not a senile change; for although absent in young children of both sexes, it is present in the male at puberty, being clearly defined in male joints of fourteen to fifteen years. Often it is double; the second eminence being situated immediately behind the first. Occasionally the whole joint surface is in addition convex, a condition first described by Faraboeuf. This tubercle is not found in every male joint, but it is present in a proportion large enough (88 per cent.) to warrant the assumption that it is an accessory factor which aids materially in promoting the strength and stability of the articulation.

The normal male joint therefore is of the diarthrodial type, possessing slight mobility only, but great strength, which is promoted by interlocking of the bony and cartilaginous surfaces, both by extra and intra-articular tubercles. In most cases it loses its movement altogether after middle age, becoming osteo-arthritis, and ankylosed.

In the *case of the female*, pregnancy has a great influence on the incidence of sacro-iliac diseases and injuries, owing, among other things, to the increased mobility of the joint at that period. Examination of a number of specimens obtained from post mortem subjects at various stages of pregnancy, showed quite clearly, that at full term, the range of movement is increased approximately two and a half times above the maximum degree present in the non-pregnant woman. This increase takes place gradually; and at the fourth month is easily recognisable. During the seventh, eighth and ninth month the mobility increases rather more rapidly. Some idea of how much movement is present at term, can be gathered from a specimen taken from a woman who died with acute inversion of the uterus. In this case, besides showing an increase range of normal rotatory movement, the ligaments and capsule were so lax that the anterior margin of the joint surfaces could be separated from each other in a horizontal plane for a distance of almost a quarter of an inch on each side.

After parturition the joint returns to its normal state but slowly, thus at the eighth week it is still lax, and not until the third or fourth month, has stability been completely regained. The mechanism of uterine involution is at present imperfectly understood; similarly with post partum changes in the pelvic joints. A specimen obtained from a woman who died four months after labour and had suffered from uterine subinvolution, showed remarkable freedom of movement, more than double the amount present in the joint of a normal pregnant woman at the same period. It would be out of the question to base an assumption on one single example, but it is interesting to note the possibility, that the two processes, of uterine involution on the one hand, and the return of stability of the pelvic joints after pregnancy on the other, may be in some way interrelated.

### 3. *The Action of the Joint in Relation to Movements of the Spinal Column.*

The functions of this pelvic joint are twofold. It must be well adapted for the transmission of the weight of the trunk to the lower limbs, and it undoubtedly provides a buffer to diminish the force of sudden jars and jolts from the lower limb. Further, during the course of dissection, evidence was sought for, in support of the view, that the joint takes part in both sexes in movements of the lower spine. In the lower apes such as *Rhesus Macacus*, also in the infant, and in the pregnant woman, this does occur; and although at present there is no direct evidence in support of it, there is reason to believe that the same thing takes place in the adult, but to a smaller degree. The range of movement is of necessity very slight in amount, and corresponds approximately to that occurring between the bodies of the adjacent vertebrae. In support of this view are the following facts. A direct relation was observed between the degree of movement at the lumbo-sacral and sacro-iliac joints. Thus when the latter was ankylosed, a thickening of the ilio-lumbar ligament, and compensatory freedom of movement at the lumbo-sacral joint were present. Expressed in figures, 81 per cent. of the thirty-eight ankylosed joints examined showed a very free range of movement much in excess of the normal at the lumbo-sacral joints. The other 19 per cent. showed ankylosis at both the sacro-iliac and ilio-lumbar joints, but compensatory increased mobility of the lumbar spine.

Those showing slight movement at the sacro-iliacs had increased mobility at the ilio-lumbar joints in only 50 per cent. of cases less marked than in the ankylosed specimen, whereas those with free sacro-iliac movement showed a correspondingly slight degree of mobility at the ilio-lumbar joint. Specimens showing the reverse condition, namely ankylosis of the ilio-lumbar joint associated with very free movement at the sacro-iliac joint have so far not been obtained, but one specimen exhibited restriction of movement at the right hip due to tubercular disease, with an unusual degree of compensatory laxity at the sacro-iliac joint. That ankylosis leads to compensatory movement of adjacent articulations, is significant evidence in support of the probability that the joint functions in the movement of the spine as a whole, and in the maintenance of the general flexibility and free mobility from occiput to coccyx.

### 4. *Structure of the Joint.*

The much discussed question of the size and situation of the joint cavity proper will be dealt with but briefly. It is doubtful whether Quain's description, in which he mentions irregularities of the joint surfaces containing glairy fluid, can be applied to other male joints of advanced age. Indeed, as already mentioned, there is every reason to regard this condition as pathological. Certainly in younger subjects of both sexes the joint surfaces are quite smooth and separate, and the presence of congenital fibrous strands bridging across the joint described by Henri Vignes must be an extremely rare condition. The joint is roughly L-shaped, but subject to considerable variation, as shown in

Fig. 3, the most constant being the presence of a third small inferior limb at the lower end, and passing backwards at right angles from the descending



Fig. 3. Third or Inferior Limb.



Fig. 4. Rods under Synovial Membrane.

limb. This third limb, as described by Humphrey, is derived probably from the third sacral segment. It is much more common in the female, over 95 per cent. of the specimens examined in this series being of that sex. The average



surface area of the joint is at birth 1.5 sq. cms., at puberty 7 sq. cms. and in adults  $17\frac{1}{2}$  sq. cms., slightly less extensive in the female. The articular cartilage is hyaline in nature. The synovial membrane is difficult to identify, or demonstrate (Fig. 4). A repetition of Albee's experiment, using in this case coloured gelatin, instead of coloured water, to distend the joint cavity, has left no doubt that the synovial membrane forms a continuous layer, attached to the margins of the articular cartilage throughout, as in any other joint cavity. This observation has been confirmed by numerous microscopical sections, taken at different levels in both limbs, in both male and female joints. They show in every case a fringe of synovial membrane, attached to the edge of the cartilage. Finally a specimen of infective arthritis of the joint showed the hypertrophied inflamed synovial membrane, and the various component parts of the articulation responding to infection in the same way, as in any other joint.

#### SUMMARY.

The old description, that the joint was an amphiarthrosis, was the description of a pathological change. The normal joint is of the diarthrodial type and in all probability takes part in movements backwards and forwards of the lumbar spine. Male and female joints are quite distinct in function and mobility for whereas the former is built for strength, aided by the presence of extra- and intra-articular tubercles, the latter is altered to meet the requirements of parturition by an increase in mobility, thereby assisting in the enlargement of the pelvic brim, to accommodate the passage of the foetal head. This it does by movements in a transverse direction as well as the rotatory movement described by Walcherew. The joint cavity itself is well defined with a continuous fringe of synovial membrane, and, at times, the addition of an accessory limb. It is a diarthrodia joint resembling in every characteristic any other joint of this type, becoming amphiarthrodial only under certain pathological conditions.

In conclusion I should like to thank Professor Johnston for much helpful criticism and the interest he has taken in the work. I am also very much indebted to Mr W. C. Hancock, Senior Assistant in the Anatomy Department of Guy's Hospital Medical School, for his invaluable assistance in the selection and preparation of material.

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# OBSERVATIONS ON THE ANATOMY OF THE HEART, LUNGS AND RELATED PARTS OF CERATOPHRYS<sup>1</sup>

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THE material described in this paper was placed at my disposal by Prof. J. P. Hill, F.R.S. It comprised the anterior part of a large *Ceratophrys* collected at Mimosa in Brazil during the Percy Sladen expedition in 1913. Prof. Hill suggested that I should work out the anatomy of the heart, lungs and related parts. I take this opportunity of expressing my deep indebtedness to him for the kindly interest he evinced throughout this piece of work and to Prof. D. M. S. Watson, F.R.S., for helping me in the interpretation of the wax model of the heart. I am obliged to Mr F. T. Pittock of the Zoological Laboratory for the photographs and to Mr P. H. Johnson for help with literature.

My object in carrying out this investigation has been to study the structure of the heart, and allude in passing to such of the interesting finds in the structure of other organs, viz. lungs, parathyroid gland, thyroid gland, carotid gland and the hyoid apparatus.

## THE HEART.

The heart is typically Anuran in character. Ventrally the pericardial membrane bears a mass of fatty tissue which forms a yellowish-looking prominence. The ventral surface of the heart is more or less convex with a ridge slightly to the right of the median line; the dorsal surface is devoid of any ridge and is more or less flat. The ventricle is divided from the auricles superficially by a groove running transversely, and from near the base of the right part of the ventricle springs the conus arteriosus. The auricles are thin-walled chambers. The sinus venosus is a very thin-walled chamber which leads by a small sinu-auricular aperture into the right auricle. The conus arteriosus, which is very short, does not pass into a bulbus aortae, but continues further forward without much apparent change in size and diameter and divides into two great arches. Each of these arches divides into three vessels, the most anterior, the carotid arch; the middle, the systemic arch; and the posterior, the pulmo-cutaneous arch.

(a) The carotid arch, the smallest of the three, soon gives off a branch, the lingual, and runs forward as the carotid artery. There is a particularly well-developed carotid gland at the point of division of the artery into two, which

<sup>1</sup> Approved as a thesis for the degree of Master of Science in the University of London.

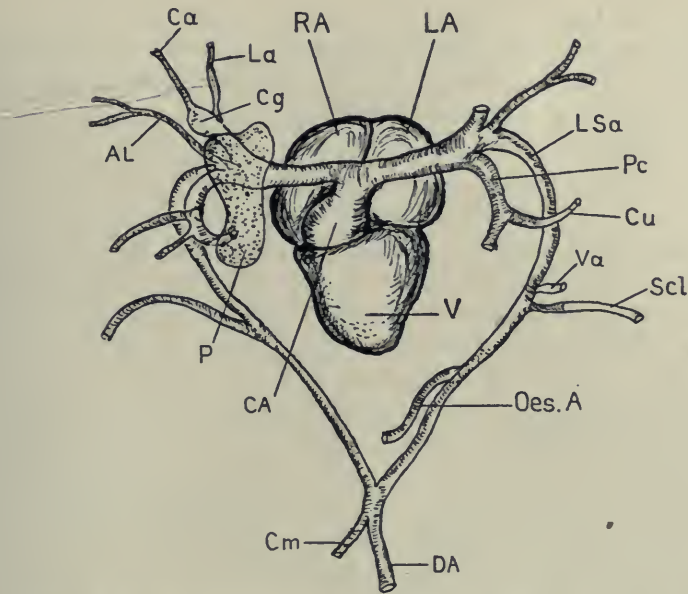


Fig. 1. Drawing of the heart (ventral view, pericardium has been removed). *A.L.* arteria laryngea, *C.A.* conus arteriosus, *Cg.* carotid gland, *C.M.* caeliaco mesenteric artery, *Cu.* cutaneous artery, *D.A.* dorsal aorta formed by the union of right and left systemic arches. *L.A.* left auricle, *La.* lingual artery, *Oes.A.* arteria oesophagea, *P.* parathyroid, *P.C.* pulmo-cutaneous arch, *R.A.* right auricle, *L.S.A.* left systemic arch, *Scl.* subclavian artery, *V.* ventricle, *Va.* vertebral artery.

is said to offer great resistance to the flow of blood in the first phases of ventricular contraction. The carotid gland is an oval swelling on either side on the carotid arch. The carotid artery enters into and emerges from it. After its entrance into the gland, the carotid artery splits up and its lumen rapidly becomes much reduced. The whole substance of the gland is cavernous with an irregular meshwork of capillaries, each provided with an endothelial lining formed by simple squamous epithelium. The substance of the gland between the capillaries is formed of a connective tissue which is not markedly fibrous. Lying in the tissue toward one end of the body are large numbers of cells apparently nearly equidiametric, with medium sized deeply staining granular nuclei; the cytoplasm is eosinophilic and richly loaded with large, deeply staining basophil granules. These cells appear to agree with certain of the leucocytes which are to be seen in the blood; and are, indeed, probably migrant leucocytes.

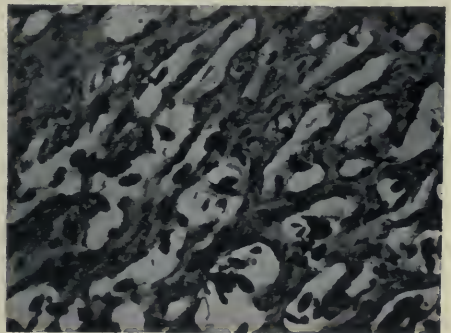


Fig. 1a. Photograph of transverse section of carotid gland to show its cavernous nature.



The whole structure is surrounded with a sheath of unstriated muscle which is continuous with that of the carotid artery. The studies of Marshall and Maurer show that in development the structure arises in part from the carotid arch at the front of the junction of the afferent and efferent parts and from an epithelial mass arising from the endoderm of the third branchial pouch.

(b) *The systemic arch*, by far the largest and stoutest, early separates from the carotid and curves round the oesophagus to descend into the abdominal cavity where it unites with its fellow from the other side to form the dorsal aorta. The systemic arch gives off a number of branches which supply the various organs. Mr L. R. Crawshay has given a very careful and detailed description of the arterial system of certain Anura. In *Ceratophrys*, the *arteria laryngea* has the same position as in *Rana hexadactyla* and leaves the systemic arch opposite the carotid gland, and is of fair size. The *occipito-vertebralis* has the normal relations. According to Mr Crawshay the a. oesophagea arises from the base of the *occipito-vertebralis* in *Rana clamata*, *R. hexadactyla*, *R. tigrina*, *Bufo mauritanicus* and *B. boreas*. But in *Ceratophrys* the a. oesophagea arises from a different level almost midway between the subclavian artery and the root of the dorsal aorta. The subclavian artery arises in close proximity to the *occipito-vertebralis* and is of fair size, though in *Rana hexadactyla* and *R. temporaria* they arise at a short distance from each other. The dorsal aorta soon gives off from near its root a large *coeliaco-mesenteric* artery. The distribution of the various branches of the arteries from the dorsal aorta as also from the subclavian artery could not be studied in my specimen.

(c) The *pulmo-cutaneous arch* is slightly smaller in size than the systemic arch and supplies the lungs and the skin; the cutaneous artery is given off from very near the point of entrance of the pulmonary artery into the lung.

(d) The *pulmonary vein*. The blood from the lungs is returned to the heart by the pulmonary veins. The two veins unite to form a fairly long trunk before entering the left auricle.

The factors of the post- and pre-caval veins could not be studied in my specimen.

*Anatomy of the heart.* The heart consists of the following parts:

- (a) The sinus venosus.
- (b) The right and left auricles.
- (c) The ventricle.
- (d) The conus arteriosus.

(a) *The sinus venosus* is a very thin-walled sac opening into the right auricle by the *sinu-auricular aperture* situated on its dorsal wall. The *sinu-auricular aperture*, which is a transverse, oval slit, is provided with two slightly curved membranous valves, one cranial and the other caudal. The cranial valve overlaps the caudal to a small extent.

(b) *The right and left auricles*. The auricles are large chambers separated by a thin, complete septum. Structurally the septum is composed of fibrous connective tissue containing granular cells and through which the sparse

muscle fibres pass. The tissue is not perforated by blood vessels and is coated with endothelium. It has two strands of neuromuscular tissue; one of these can be traced to one of the auriculo-ventricular valves. Although not in a condition for detailed description the strands appear to be composed of ordinary Purkungi cells in addition to the nerves and ganglion cells.

The walls of the auricles though thin are thicker than the septum and the right auricle has larger capacity than the left. The septum dividing the auricles becomes narrower and narrower and ends in a concave free border so that the two auricles open into the ventricle by a common auriculo-ventricular opening.

*Valves.* The auriculo-ventricular aperture is guarded by well developed valves. These valves consist essentially of a very large ventral membranous

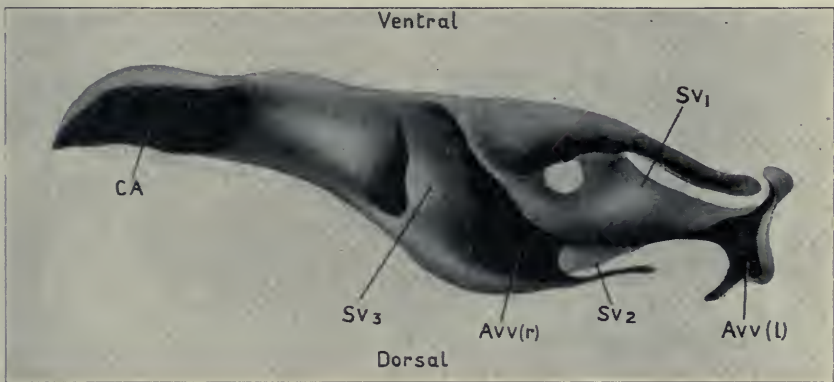


Fig. 2. Drawing of the auriculo-ventricular valves (from wax model, cut surface viewed from the caudal aspect of the heart). *A.V.V. (r.)* auriculo-ventricular apertures leading to the right auricle, *A.V.V. (l.)* auriculo-ventricular apertures leading to the left auricle, *C.A.* aperture leading to the conus arteriosus, *S.V.<sub>1</sub>* large membranous semilunar valve (ventral) guarding the auriculo-ventricular aperture, *S.V.<sub>2</sub>* smaller semilunar valve (dorsal), *S.V.<sub>3</sub>* semilunar valve situated on the roof of the ventricle between the auriculo-ventricular opening and the opening of the conus arteriosus. (N.B. The chordae tendinae are not shown in the diagram.)

flap (Fig. 2, *S.V.<sub>1</sub>*) which is attached along a line which is concave posteriorly. The attachment on the left extends caudally for some distance. The free margin is imperfectly divided into right and left portions. The much smaller dorsal valve (Fig. 2, *S.V.<sub>2</sub>*) is attached to the septum and runs caudally so that the free margin which lies on the right is almost longitudinal. In addition there is a small membranous pocket valve (Fig. 2, *S.V.<sub>3</sub>*) rising from the roof of the ventricle between the auriculo-ventricular opening on the left side and that of the conus arteriosus on the right side. Viewed from in front the auriculo-ventricular aperture does not present any valvular structure on the left side. Sections of *Rana temporaria* and *Bufo vulgaris* show the presence in them of three auriculo-ventricular valves agreeing with those of *Ceratophrys*. The small third valve does not appear to have been described in any Anuran.

(c) *The ventricle.* The ventricle is conical in shape and has a very thick and



muscular wall. The cavity of the ventricle is divided into a number of small confluent chambers of varying size by muscular trabeculae. There is no inter-ventricular septum comparable to that of the hearts of birds and mammals. In addition to the auriculo-ventricular passage, there is a passage which leads to the conus arteriosus. I have not studied the architecture of the heart muscles.

(d) *The conus arteriosus.* The nomenclature of the great trunk, given off from the base of the ventricle, is in some confusion. The term "conus arteriosus" was first introduced by Gegenbaur who used it to denote the region between the ventricle and the ventral aorta in Elasmobranch fishes and Ganoids and to distinguish it from the bulbus arteriosus of Teleosts. Huxley, in describing the amphibian heart, says: "The heart consists of two auricles, a single ventricle and a *bulbus arteriosus*....The walls of the bulbus arteriosus contain striated muscle fibres and are rhythmically contractile. Valves are sometimes placed at each end of it and it may be imperfectly divided into two cavities by an incomplete longitudinal septum." This account of Huxley's is correct both as to facts and nomenclature. Ecker makes out four divisions of the heart one of which he terms "truncus arteriosus." Gegenbaur adopts the term "muscular bulb" to denote the "bulbus arteriosus" of Huxley. Marshall, in the frog, identifies the "bulbus arteriosus" of Huxley as the "truncus" but notes two regions thereof, a proximal part, the pylangium, which is a single vessel arising from the ventricle, and a distal part or synangium, which consists of the basal parts of the aortic arches closely bound together, while Rolleston follows the terminology of Ecker and Marshall. Parker and Haswell adopt the terms conus arteriosus to designate the pylangial part of the truncus arteriosus or the proximal part of the bulbus arteriosus, and the bulbus aortae to designate the distal part of the great trunk to which the name synangium is given by Marshall and the term truncus arteriosus is applied in the common language of texts. Miss Oliver in describing the Australian frogs uses the term truncus arteriosus to indicate the bulbus arteriosus of Huxley. The truncus arteriosus is equivalent to the ventral aorta or cardiac aorta and is not invested by cardiac muscle. However, the part designated "truncus" in fishes is not homologous with the part in frogs. In frogs in the truncus region there are a group of vessels bound together while in fishes it is a single vessel. If priority has any value in zoological nomenclature consistent with its significance the term "bulbus arteriosus" of Huxley should be unhesitatingly adopted but "a bulb" is not of universal occurrence and as such is of very restricted use. The term conus arteriosus seems to be the more satisfactory and is the term used to designate the entire vessel in this paper. Though a pylangial and synangial region could not be made out in this very shortened conus arteriosus superficially by any indication of a groove, yet the terms are used to denote the proximal and distal parts of the conus arteriosus. Structures in those regions are described with reference to pylangium and synangium respectively.

The conus arteriosus has suffered a great deal of varied description as



regards its structural details, and a glance at the following table will convince one of the considerable differences of opinion held by leading authorities.

Table showing the number of valves, etc., according to various authorities.

Author		Pylangial valves	Synangial valves	Position of Pylangial valves
Ecker	<i>Rana</i>	2 semilunar valves	One	Pylangial
Rolleston	<i>Rana</i>	3 semilunar valves	3, one of which is the spiral fold, two other small ones, one dorsal and one ventral. A vertical septum placed transversely divides the origin of the pulmonary arch from the origin of the systemic and the carotid arches	Pylangial
Sedgwick	<i>Rana</i>	3 semilunar valves	3 semilunar valves	Pylangial
Bourne	<i>Rana</i>	2 semilunar valves	3, to one of which the spiral valve is fused and the smallest of the 3 valves	Pylangial
Parker and Haswell	<i>Rana</i>	3 small semilunar valves	1 valve and the free end of the longitudinal valve	Conus (Pylangial)
Miss Oliver	<i>Hyla aurea</i>	2 laterally placed semilunar valves	1 plus 1 small valve	Pylangial
Miss Oliver	<i>Cystignathidae</i>			
	(a) <i>Limnodynastes dorsalis</i>	2 valves with distinct papillae	Two	Pylangial
	(b) <i>Heleioporus pictus</i>	2 with small papillae	2 indistinct. The interior locking apparatus most indefinite in this genus	Pylangial
	(c) <i>Chiroleptes alboguttatus</i>	Two	1 distinct and 1 poorly developed	Pylangial
	<i>Bufonidae</i>			
	(a) <i>Notaden bennetti</i>	2 with no papillae	Two	Pylangial
	(b) <i>Pseudophrynae Semimormorata</i>	?	Two	Pylangial
Gaupp	( <i>Rana esculenta</i> )	Three	3 and 2 half-valves	Pylangial

It will be clear that all are agreed as regards the existence of the spiral valve while there is apparently no agreement as regards the number and disposition of the pylangial and synangial valves.

The structure of the conus arteriosus as determined by an examination of transverse sections is as follows:

(a) *The inner coat.* This is lined by well defined endothelial cells whose nuclei stain fairly deep. Exterior to the endothelial lining there is a connective tissue network.

(b) *The middle coat.* The middle coat is remarkably well developed and consists of muscle fibres disposed circularly. These fibres are of moderate length. The muscle fibres do not seem to form a complete ring. The nuclei are elongated and sometimes thrown out of shape due possibly to shrinkage. These fibres are transversely striated. Some such trans-striated fibres may be found even in the synangial region.

(c) *The outer coat.* This layer is formed mostly of elastic tissue. There is

a great concentration of this tissue near the middle coat and the fibres become rarer as the surface is approached.

In my specimen the exact distribution of the involuntary muscle fibres in the conus arteriosus could not be studied and as such no regional differentiation based upon the differences in structure could be made although it is maintained by some authorities that the proximal region of the conus arteriosus contains cardiac muscle fibres and the syngangial part does but contain muscular fibres of the plain variety.

For purposes of accurate description a wax model of the conus arteriosus and the base of the ventricle was reconstructed from serial sections of  $15\mu$  thick at a magnification of 25.

### THE CONUS ARTERIOSUS.

The conus arteriosus arises in *Ceratophrys* as in other amphibia from the base of the ventricle. For the sake of clearness the conus arteriosus is described as if the two segments—pylangium and syngangium—were distinct. In Fig. 3 are shown the main features of the conus arteriosus.

*The pylangium.* The opening into the cavity of the conus arteriosus from the ventricle is guarded by two very well developed valves—a right and a left semilunar valve (Fig. 3a, *S.V.*<sub>2</sub>, *S.V.*<sub>1</sub>). These valves are fairly broad and their free margins face towards the cavity of the conus. The valves are composed of fibrous connective tissue continuous with that of the wall of the conus. The free margins of these valves are continued cranially in a gradually sloping manner and project freely into the cavity of the conus arteriosus. The cranial extension of the free margin of the left semilunar valve lies close against the right margin of the longitudinal spiral valve; a dorsal valve is present but is rudimentary and does not appear to have any functional significance (Fig. 3a, *S.V.*<sub>3</sub>).

*The spiral valve* (Fig. 4). In the pylangial segment, the cavity of the conus arteriosus is divided incompletely into two cavities (cavum aorticum, and cavum pulmo-cutaneum) by the spiral valve which has attained large dimensions. Owing to the peculiar twist the spiral valve has, the position of the cavum aorticum which is dorsal to the cavum pulmo-cutaneum at first, becomes ventral to the pulmo-cutaneum as the cranial end of the conus arteriosus is reached. The remarkably strong spiral valve runs cranially along the entire length of the pylangium. The valve is fixed dorsally and is free ventrally. The line of attachment of the spiral valve indicates more or less the axis of the spiral described by the conus arteriosus itself. The valve arises at the left ventral margin of the entrance into the conus arteriosus from the ventricle. Owing to the spiral arrangement of the valve, cranially it passes into the dorsal wall of the conus though caudally it arises from the base of the left ventral semilunar valve. The spiral valve forms a very distinct longitudinal ridge, the free border of which begins caudally at the beginning of the conus arteriosus and crosses obliquely to the left. In the caudal region its free margin is carried

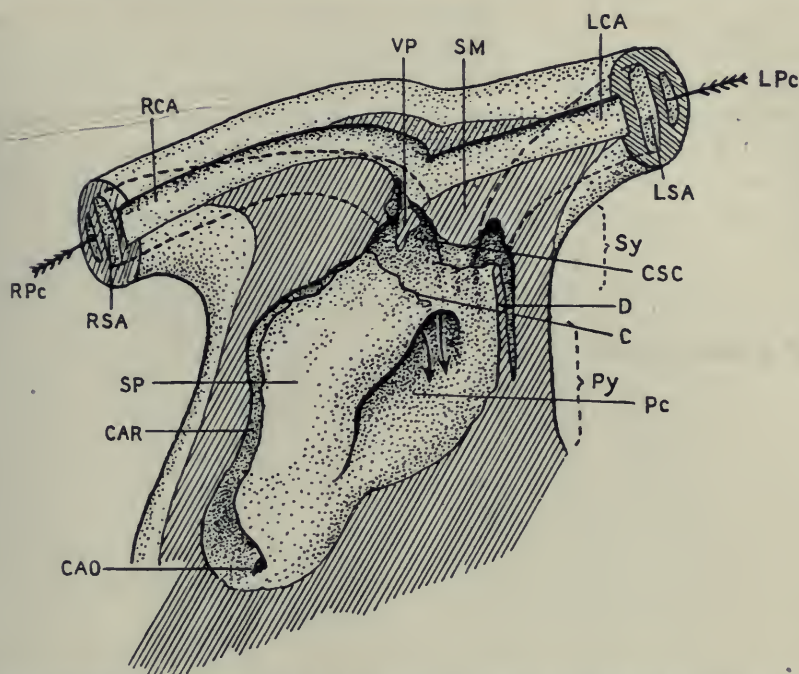


Fig. 3. Drawing of a sectional view of the conus arteriosus (ventral lateral view, from model). *C.* cup-like valve at the cranial end of the spiral valve, *CAO.* aperture leading into the conus arteriosus from the ventricle, *CA.R.* cavum aorticum, *C.S.C.* cavum systemico-carotideum, *D.* large semilunar valve, *L.P.C.*, *R.P.C.* left and right pulmo-cutaneous arches, *L.S.A.*, *R.S.A.* left and right systemic arches, *L.C.A.*, *R.C.A.* left and right carotid arches, *SP.* spiral valve, *S.M.* septum medianum, *V.P.* valvula paradoxa (cut surface), *Py.* pylangium, *Sy.* syngangium. The three semilunar valves at the base of the conus arteriosus are not shown. Cavum pulmo-cutaneum ends blindly caudally and opens by a wide opening into the cavum systemico-carotideum anteriorly, while the cavum aorticum communicates directly with the ventricle caudally and has a very narrow passage anteriorly into the cavum systemico-carotideum.

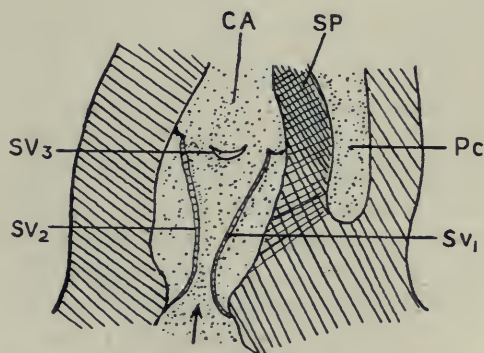


Fig. 3a. Section (diagrammatic) across pylangium to show the valves at the base of the conus arteriosus. *S.V.<sub>1</sub>* left semilunar valve, *S.V.<sub>2</sub>* right semilunar valve, *S.V.<sub>3</sub>* dorsal semilunar valve, *S.P.* spiral valve, *P.C.* cavum pulmo-cutaneum.



by a flange bent towards the right, while cranially it is bent to the left. Finally the free border fuses with the left wall of the conus arteriosus, while the attached border of the spiral valve is continuous with the right wall. The special relations of the cranial part of the spiral valve indicated above lead to an interesting disposition of the divisions of the conus arteriosus. The originally ventral cavum pulmo-cutaneum now becomes dorsal to the cavum aorticum, which is gradually shifted from a dorsal to the ventral position. The ventricle

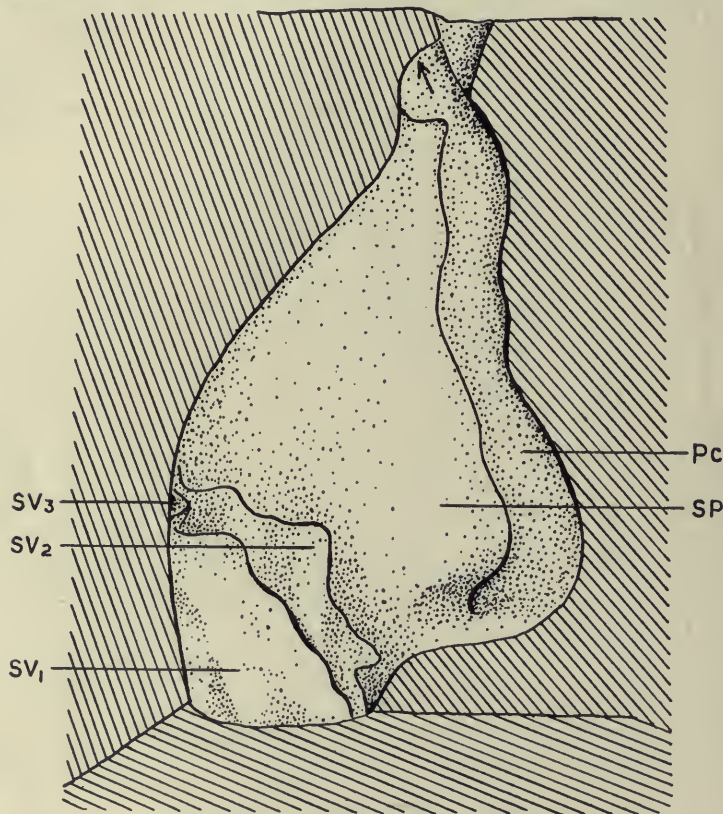


Fig. 4. Drawing of the model to show the spiral valve, *SP*, and the semilunar valves at the base of the conus arteriosus, *S.V.*<sub>1</sub>, *S.V.*<sub>2</sub>, and *S.V.*<sub>3</sub>. *S.V.*<sub>3</sub> is very small. *P.C.* cavum pulmo-cutaneum. The arrow at the cranial end indicates the passage to the pulmo-cutaneous arch. The spiral valve itself becomes smaller as it reaches the cranial end of the conus arteriosus.

leads directly into the cavum aorticum and the cavum pulmo-cutaneum is brought into communication with the ventricle only through the cavum aorticum round the free margin of the spiral valve. The cavum aorticum which is very wide at first rapidly narrows, while the cavum pulmo-cutaneum which is narrow at first enlarges as rapidly, and leads to the pulmo-cutaneous arch and also to the cavum systemico-carotideum.

### THE SYNANGIUM.

The cranial segment of the conus arteriosus may be described as the synangium. The two pulmo-cutaneous arches unite in the synangium to form a common trunk which is separated from the cavum systemico-carotidium by the septum principale (*Sp.* Fig. 5) and which passes caudally to open by a single aperture into the dorsal wall of the cavum pulmo-cutaneum in the pylangium. The cranial margin of the opening is formed by the free margin of the septum principale which is obliquely placed, its left end lying much cranial of its right attachment. This opening is guarded by two valves which lie actually within the pulmo-cutaneous trunk and a third lying in the cavum pulmo-cutaneum plays also an important part in regulating the supply of blood to the arches. The valves within the pulmo-cutaneous trunk are “*d*”

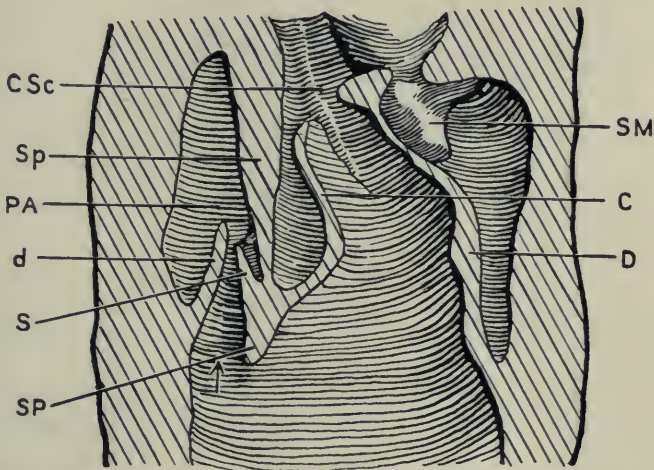


Fig. 5. Sectional view of the model of the conus arteriosus. *C.* large cup-like valve on the spiral valve, *D.* large semilunar valve, *SP.* cut surface of the spiral valve, *Sp.* septum principale separating the pulmo-cutaneous arch from the cavum systemico-carotideum (*C.S.C.*), *S.M.* septum medianum, *P.A.* pulmo-cutaneous arch. The arrow indicates the path leading into the pulmo-cutaneous arch. *S.* small semilunar valve (dorsal), *d.* semilunar valve (ventral). Valves *S* and *d* guard the entrance into the pulmo-cutaneous arch. The valves at the base of the conus arteriosus are not shown in this figure.

(Fig. 5, *d*), which is attached to the dorsal wall and has its free margin directed cranially, and “*S*” (Fig. 5, *S*), which is attached to the ventral wall formed by the septum principale, and also has a cranially directed free edge.

Fig. 6 shows the position of the pulmo-cutaneous arch and the relative sectional sizes of the cavum pulmo-cutaneum and cavum aorticum.

The opening into the left systemic can only be reached by passing over the dorsal part of the cranial margin of valve *D* (Fig. 3, *D*). The left systemic is separated from the common trunk of the right systemic and the carotids by the septum medianum (Fig. 3, *S.M.* and Fig. 5, *S.M.*), the caudal end of which hangs free as a rounded boss in the cavity of the valve *D* (Figs. 3 and 5, *D*), whose free margin lies on the left side of it. The plane of the septum medi-

anum is at right angles to that of the septum principale. The left carotid arch opens into the right systemo-carotid chamber by a very narrow slit cranial of the semi-independent opening of the right carotid arch. Immediately below the entrance from the synangium to that part of the opening of the common carotids and the left systemic, which leads most directly into the carotids, lies the valvula paradoxa of Gaupp (Fig. 7, *V.P.*). This consists of a small but thick fibrous flap attached to the ventral wall of the extreme cranial end of the synangium, its free margin lying very near to the septum medianum and the free margin of valve *D*.

The right systemic, and the right and left carotids have a common entrance from the cavum pulmo-cutaneum forming indeed the direct continuation of

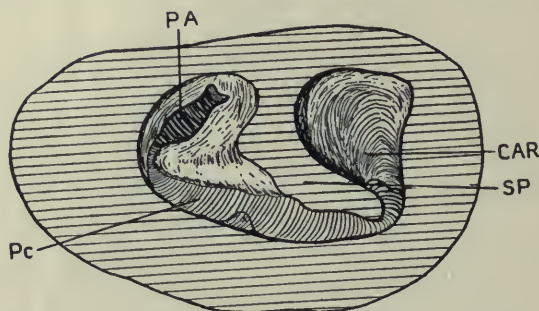


Fig. 6. Drawing of section of the model of conus arteriosus, seen from the caudal aspect. *P.A.* pulmo-cutaneous arch, *CAR.* cavum aorticum, *SP.* spiral valve, *P.C.* cavum pulmo-cutaneum.

that cavity. The opening is guarded by three valves, *C*, *D* and *E*. The valve *C* (Figs. 3 and 5) arises from the cranial end of the spiral valve, that surface which faces the lumen being continuous with the surface of the spiral valve which forms part of the cavum pulmo-cutaneum. The cavity behind the valve is bounded by the lower end of the septum principale which is itself directly continuous with the cranial end of the spiral valve. Valve *D* is a very large pocket valve attached to the left dorso-lateral portion of the wall of the synangium lying in the cavum pulmo-cutaneum, the ventral part of its free margin extending up to the extreme cranial end of the synangial cavity. The valve is of very large size, the space enclosed between it and the wall of the synangium being very capacious. Valve *E* is a very small pocket valve attached to the ventral wall of the synangium between the ends of *C* and *D*. The valve *E* is not shown in Fig. 3.

#### FUNCTION OF THE VALVES.

*The sinu-auricular valves.* The sinu-auricular valves prevent the backflow of blood from the right auricle to the sinus cavity during auricular systole.

*The auriculo-ventricular valves.* The function of these valves is to prevent regurgitation of blood from ventricle to the auricles during ventricular systole.



*The pylangial valves.* As is well known, the ventricle of the amphibian contains both venous and arterial blood, and the venous blood which is in the right part of the cavity first finds access to the cavum aorticum because of the position of the opening of the ventricle into the conus (Fig. 2, *C.A.*) but as this cavity narrows very quickly into a small slit, most of the blood is forced round the free margin of the spiral valve into the cavum pulmo-cutaneum and only a small quantity can enter the carotico-systemic chamber directly. As the cavity of the conus is less than that of the ventricle some blood must pass on to the arches during continuance of the ventricular systole. During this process the conus becomes expanded and a wide passage is left between the free margin of the spiral valve and the ventral wall.

At the end of the systole of the conus all the aortic arches are filled with blood under pressure, their cavities being enlarged; this pressure is maintained by the elasticity of the walls of the arteries and at the beginning of the diastole of the conus results in a closure of all the valves guarding the entrances to the arches from the conus.

The arterial pressure which maintains the closure of these valves falls off as the blood is forced forward through the arteries and it seems obvious that the reduction in pressure will take place more rapidly in the pulmo-cutaneous arch than in the other arches, because the capillary area of that arch is so much smaller than those of the systemic and the carotid arches.

Thus a pressure of blood in the conus which will be sufficient to open the valves guarding the pulmo-cutaneous arch will be insufficient to open the other valves. As blood is forced into the pulmonary arch, the pressure in it gradually rises until it equals that in the carotico-systemic system in which the pressure has been falling; when this is the case the valves guarding the latter system will open and blood will be forced into the carotico-systemic chamber almost to the exclusion of the pulmo-cutaneous arch which is now full of blood. This pressure will force the blood into the carotico-systemic chamber, passing the valves *D*, *C* and *E*. Some blood passes across the margin of the valve *D* and enters directly the left systemic.

Once the blood has passed these valves, it lies in a chamber into which open the left systemic arch and the right systemo-carotid trunk.

On account of the small size of the carotids, and the presence on them of the carotid glands compact rete mirabilia, it appears probable that the pressure in the carotids will drop more slowly than that in the systemic trunks which will thus be filled first.

As the two systemic arches appear to be of the same diameter and join symmetrically to form the dorsal aorta, it would appear that the pressure in them at their origin from the synangium should be equal but as the left systemic more directly continues the cavity of the synangium, it is probable that it will at first receive a larger supply of blood than the right and be filled first, i.e. with mixed arterial and venous blood.

Finally when the pressure in the carotico-systemic chamber rises sufficiently

blood will be forced up the carotids. The left carotid has a direct course continuing the lumen of the synangium and would thus tend to receive a larger supply than the right which turns sharply over, shortly after its exit.

Three vessels and especially the right are connected with the right systemic by a very narrow channel. Disregarding this connection, they may be seen to open out of the carotico-systemic chamber from two small recesses which are separated by the *valvula paradoxa* and it appears probable from its shape that this valve seems to equalise the amount of blood flowing on into the carotids. It is probable that at or about this time, the systole of the conus begins closing the valves guarding the entrance from the ventricle and leading to an increased pressure. This blood flowing into the carotids is the last to leave the heart and hence the last to enter the conus and is arterial blood.

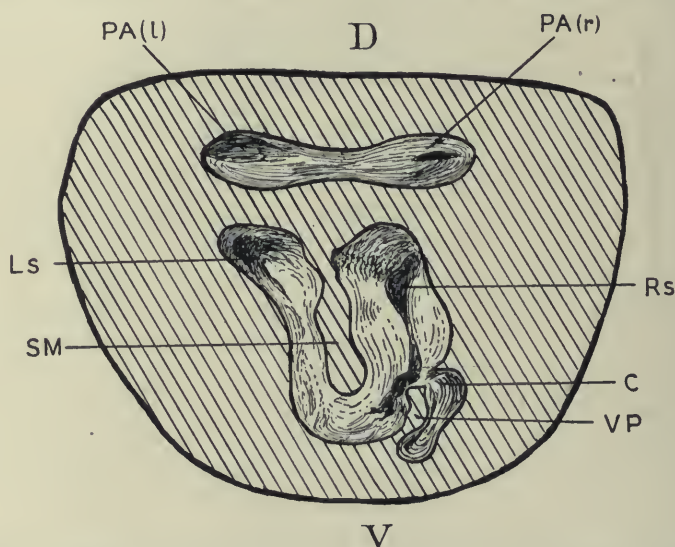


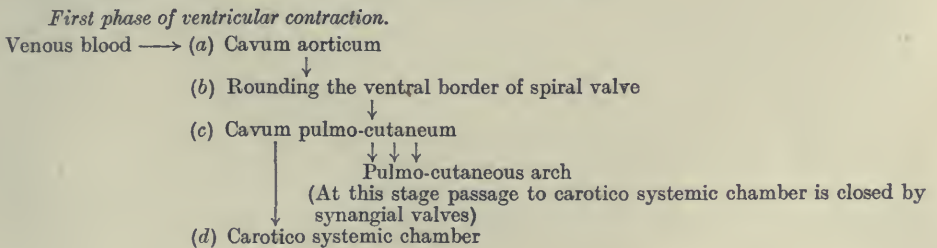
Fig. 7. Drawing of section of the model of the conus arteriosus seen from the caudal aspect. P.A. (l.), P.A. (r.), left and right pulmo-cutaneous arches, L.S. left systemic arch, R.S. right systemic arch, C. entrance to carotid arch, V.P. valvula paradoxa.

*The spiral valve* (Fig. 4). The function of the spiral valve has been a subject of much discussion. It is not unreasonable to suppose that its main function is to direct the flow of blood. In other words it prevents by judicious regulation of the blood, the over-distension and the consequent haemorrhage of the lungs. That this view is probably correct is seen from the following. In fishes the heart is purely venous and has no chambers for the arterial blood, the necessity for the division of the auricles is not indicated and there is no spiral valve as such in the bulbus aortae; but with the assumption of aerial respiration the heart undergoes adaptive modifications to take up the work under altered conditions. Thus in Dipnoi, although provided with the very primitive type of lungs, there are remarkable advances made in the structure of the heart. There is already an incomplete separation of the atrium into two

chambers by the growth of an atrial septum; the conus arteriosus has similarly undergone structural changes. There is a longitudinal spiral valve formed as a result of the fusion of the cusp valves on one side. The separation of the venous from the arterial arches is effected by this valve. But in Urodela and Batrachia with fully functioning lungs we find that the auricles are separated into a right and left half for the reception of venous and arterial bloods respectively; and in these instances the conus arteriosus has a well developed spiral valve. And again in some of the Gymnophiona in which one of the lungs undergoes atrophy, we find the auricles are separated partially, cutaneous respiration coming into help. The conus arteriosus has a spiral valve which shows proportionate degeneration. And finally when we consider the case of lungless Salamanders the existence of an undivided auricle forcibly reminds one of the venous heart of the fish with the exception that the heart in Urodela does get a small return of oxygenated blood from the skin. There is a mixture of arterial and venous bloods in the auricle of lungless Salamanders. Also, it should be recalled that the degeneration of the spiral valve in the lungless Salamanders is very marked. The only inference from a consideration of structural variations mentioned above is that the inter-auricular septum separates the venous from the arterial blood either completely or incompletely in accordance with the perfect or imperfect nature of the septum and that the progressive degeneration of the spiral valve keeping pace with the loss of the inter-auricular septum and the lungs is strongly suggestive of the fact that it has, despite the denial of Dr Bruner (14), a directive function. The gradual loss of the lungs has tended not only to the loss of the inter-auricular septum but has contributed largely to the degeneration of the spiral valve.

Miss K. K. Oliver has, as a result of the study of the conus arteriosus of the Australian frogs, suggested a theory as to the mode of circulation depending upon the presence of "an interlocking apparatus and the disposition of the valves." I find great difficulty in correlating her observations with those of mine on *Ceratophrys*, *Rana* and *Bufo*, and I do not intend offering any remarks on her views. However, she does not seek to explain the course of blood in the conus arteriosus during the early and late stages of the ventricular contraction, and the function of synangial valves.

The course of the blood may be shown as follows:





*Second phase of ventricular contraction.*

Mixture of venous and arterial bloods →  
 → Carotico systemic chamber along (a), (b), and (c)  
 →  
 Blood of syngangial valves → ↓ ↓ ↓  
 Mostly to the left systemic arch  
 Right systemic receiving very little of this mixed  
 blood mainly from valve C

*Later stage and systole of conus.*

Arterial blood → (d) along (a), (b), and (c).  
 → Right systemic arch  
 ↓ ↓  
 Right and left carotids  
 (Probably the left carotid receives blood earlier than the right.)

## DISCUSSION.

It will be seen that the explanation as to the distribution of arterial and venous blood in *Ceratophrys* agrees in the main with that given by Gaupp for *Rana temporaria*. But it differs in certain respects. Gaupp says

that in the first phase of ventricular systole, the blood which flows from the right auricle streams into the cavum aorticum as well as into the cavum pulmo-cutaneum of the bulbus and truncus. It may be said with some degree of truth that in the first phase of ventricular systole the main mass of blood gets into the pulmo-cutaneum and it there finds the least opposition....The arterial blood gets into the bulbus in the second phase. The first passive stretching of the bulbar wall, by the latter, causes a contraction of the bulbar musculature. As a result of this contraction, the ventral bulbar wall approaches the free edge of the septum so as to bring about a complete separation of the two parts.

As the bulbar contraction proceeds, the left bulbar cavity is shut off from the right, and as only the right is in communication with the ostium ventriculare, the result is that during the second phase of ventricular systole, the free passage of blood is more and more restricted to the cavum aorticum. The blood column gushing up from the right, against the septum will now contribute only to pressing the septum against the opposing ventral wall, and so completely shut off the left cavity. If therefore at the commencement of the bulbar contraction some blood may chance to reach the left cavity, this in the course of the second phase ceases completely and the arterial blood of the left half of the heart comes only into the cavum aorticum. The left half of the bulbus contains as a result absolutely no blood at all in the second phase.

In Sabatier's opinion, the septum medianum plays a very important part in the distribution of blood to the systemic and carotid arches in the second phase of ventricular systole, the truncus is stretched by the inrush of blood, resulting in the separation of the ventral truncus wall, from the free edge of the hind portion of the septum medianum aorticum; and when the truncus itself begins to contract the entry into the left aortic canal will be obstructed and the blood will now flow especially to the right aortic arch. As a result there will arise from the right a pressure against the septum medianum which must now actually contribute to the closing of the left aortic arch. Sabatier, however, had not observed the presence of the swelling on the septum medianum

to explain the functional asymmetry of the aorta. Further the extremely narrow passage to the carotid arches will be closed by the action of the *valvula paradoxa* which spreads itself only when the aorta is much extended with blood at the beginning of the ventricular systole and it loses its function as the current becomes weaker. After the systemic arches have been filled, the blood, which at this time is mostly arterial in character, gets into the carotid arches.

It appears to me that neither Gaupp nor Sabatier have fully appreciated the extremely small size of the direct communication of the *cavum aorticum* with the *systemico-carotid* chamber and the much larger area of the opening with that space from the *pulmo-cutaneous* chamber.

The relative size of the passages suggest that the *systemics* and *carotids* receive most of the blood from the *pulmo-cutaneous* chamber and only a very minor part from the *cavum aorticum*.

Both Gaupp and Sabatier, from a consideration of the structural details, arrive at the conclusion that the left cavity of the *conus arteriosus* is completely shut off from the right cavity during the second phase of ventricular systole, although they are continuous during the first phase. In view of the lie of the cavities, their varying capacities and the relation of the spiral and *synangial* valves to the openings of the *pulmo-cutaneous*, *systemic* and *carotid* arches, I am led to differ from these authorities in the interpretation of the structural findings. The right dorsal cavity of the *conus* into which the right part of the ventricle communicates is very wide caudally, the left cavity being a narrow chamber.

The left cavity (*cavum pulmo-cutaneum*) obtains large dimensions as it is traced cranially and curves dorsalwards, leading to the *pulmo-cutaneous* arch on the one hand and into the *carotico-systemic* on the other.

It is well known that although the ventricle is single its right half contains venous and its left side contains arterial blood. The *conus arteriosus* springs from the right side of the ventricle. Hence during the first phase of the ventricular systole, it is the venous blood which is forced into the right part of the *conus arteriosus* and flows along, but owing to the directive action of the spiral valve, and the inner surface of the semi-lunar valves of the *pylangium*, this venous blood is directed to the left cavity which leads to the *carotico-systemic* chamber directly and indirectly into the *pulmo-cutaneous* arch. The passage of blood to the *carotico-systemic* chamber is rendered impossible by the closed semi-lunar valves guarding the *synangial* region until the pressure rises sufficiently, and so the incoming blood finding the pressure keeping the valves *d* and *S* closed small, flows into the *pulmo-cutaneous* arch (see p. 307). During ventricular systole, as the blood in the right side flows into the *conus arteriosus*, arterial blood from the left part of the ventricular cavity streams across to the right side and mixes with the remaining venous blood. Thus the blood that is pumped out during the early part of the second phase of ventricular contraction, is of a mixed character. Any blood that enters the *conus arteriosus* during the second phase enters the right cavity of the *conus* and flows into the

left, owing to the directive action of the spiral valve. Hence it may be said that the blood does not "get into the bulbus in the second phase under different conditions from those of the first."

Gaupp says:

Bei gefültem Bulbus beträgt die Höhe der septumleiste ungefähr  $\frac{2}{3}$  des Bulbus-durchmessers, bei erschlafitem, leerem Bulbus ungefähr  $\frac{4}{5}$ , und bei contraction des Bulbus, wobei sich die Bulbuswände nach der Basis des Septums als der relativ fenesten Wandepartie zusammenziehen, kommen die äussere Bulbuswand und der freie Rand des septum des zur Berührung, so dass alsdann das cavum aorticum und das cavum pulmo-cutaneum bulbi völlig von einander getrennt sind und das cavum pulmo-cutaneum hinten blind endigt, ohne communication mit dem ostium ventriculare bulbi.

It should at once be stated that in *Ceratophrys*, the left cavity of the conus always ends blindly, posteriorly, and as already described gets into communication with the ventricle only through the intermediation of the right cavity of the conus.

Further, it is hard to imagine that the spiral valve, which becomes smaller as it reaches the cranial end, could possibly form a complete and absolutely unyielding partition between the right and left cavities of the conus arteriosus. The inapplicability of Gaupp's suggestion to *Ceratophrys* becomes fairly evident, when it is realised that the carotico-systemic chamber is in direct continuity with the left cavity of the conus and if the cavity became separated from the right, during the second phase of ventricular contraction, practically no blood could get into the systemic and carotid arches. It does not seem justifiable to assume that, during the contractile period of the conus arteriosus, the ventral free edge of the spiral valve comes into contact with the ventral wall, so as to form an effective comparatively rigid partition, and cut off the left part of the cavity from all connection with the ventricle. For, in addition to the facts already mentioned, it is highly problematical, if a mass of tissue with very poor muscular contents can withstand the pressure of the intruding blood. It is open to doubt if the spiral valve, which is  $\frac{2}{3}$  the diameter when the conus is full,  $\frac{4}{5}$  when it is empty and relaxed, would form an effective partition at any period. Hence no part of the conus is, in my opinion, really devoid of blood at any given time and no such separation of the conus cavities takes place as mentioned by Gaupp.

The manner of distribution of blood to the systemic and carotid arches in *Ceratophrys* does not differ in any essential points from that of *Rana temporaria*.

#### LUNGS.

Two remarkably well developed lungs associated with the habit the frog has of puffing itself up, are present. They possess a very characteristic appearance. Each lung has the shape of a hollow conical bag measuring in its much contracted condition 35 mm. along its longer axis and 14 mm. across its shorter axis. The roots of the lungs are very narrow and each lung enlarges itself as



it recedes from its point of attachment. The lungs are covered by a delicate plenoperitoneal membrane and are spongy to the touch and the inner surface presents a honeycombed appearance. There are a number of polygonal chambers bounded by more or less cylindrical trabeculae which have attained rather large dimensions for an amphibian lung (Fig. 8). The trabeculae form a distinct network. The structure of the lung is demonstrated in a diagram of the transverse section (Fig. 8*a*) and in Figs. 8*b*, 8*c*. It will be seen that the

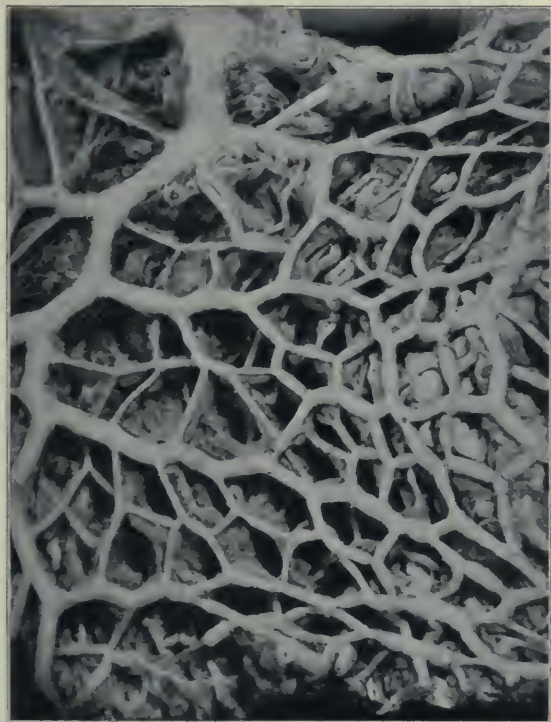


Fig. 8. Photograph of a portion of the interior of the lung of *Ceratophrys* showing the polygonal cavities bordered by well developed trabeculae.

structure of the lung is typically Anuran in character; and the following points in the structure may be referred to as being of special interest.

(*a*) The muscle tissue finds the greatest development in the trabeculae bounding the polygonal depressions. Histologically the trabeculae are composed of involuntary muscle fibres. The muscle cells are spindle-shaped with elongated and deeply staining nuclei. Extended examination shows that the muscle fibres pass from the trabecular region towards the muscular tissue found in the wall of the lung.

(*b*) I have not been able to confirm the statement that the cells near the angles of the trabeculae are columnar and ciliated.

(c) The capillaries are indeed very small and seem to be just wide enough to allow a single corpuscle though in some cases more than one corpuscle could be seen in a capillary. In exceptional cases only there are large vessels lying under the epithelial lining.



Fig. 8a Drawing of transverse section of the lung showing the muscular trabeculae, vessels and capillaries. *Mt.* muscular trabeculae, *E.* epithelial lining, *Ca.* capillaries, *V.* blood vessels.

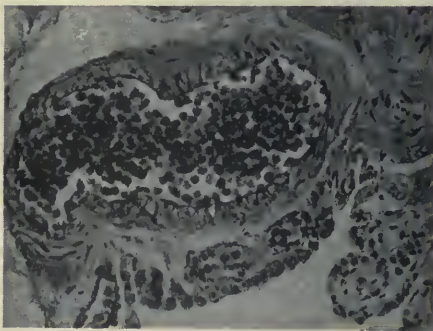


Fig. 8b. A photograph of the transection of lung to show large vessels, capillaries and epithelial layer.

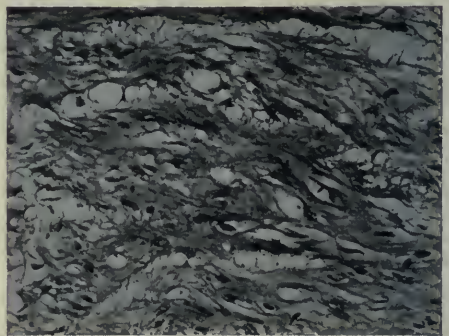


Fig. 8c. Photograph of the section of the trabeculae of the lung to show the smooth muscle fibres with pronounced nuclei.

#### THE PARATHYROID GLAND.

According to Mrs F. D. Thomson, there are in the *Anura* she has examined, usually "two small oval or rounded corpuscles on each side of the body." In *Ceratophrys*, however, there are two well developed large and greatly elongated



glands lying on either side just in front of the carotid artery and running across the arterial arches (Fig. 1, *P*).

*Histology.* Histologically the gland consists of two not very well marked regions. The cortical region was not clearly distinguishable but the tissues of the gland consist of rounded, sometimes elongated, cells with granular contents. The arrangement of these cells in certain parts reminds one of the existence of

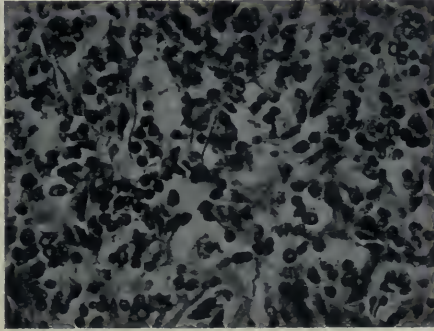


Fig. 9. Photograph of the section of parathyroid to show its general structure.

tubular structure. Whether or not they are actually tubular it is hard to state. The gland has a very rich vascular supply. Careful and extended examination reveals the existence of a few vesicular regions comparable to those of the thyroid gland but the absence of colloidal material renders the comparison of doubtful value. The intercellular tissue is of the fibrous kind and in some cases blood capillaries run by the side of what seem to be vesicular spaces.

#### THE THYROID GLAND.

There is a well developed gland on either side. The gland of each side is an oval corpuscle placed ventrally to the posterior process of the hyoid. It occupies a very concealed position. No difficulty is experienced in identifying the glands which are of the size of a small pea. Viewed with the aid of a magnifying lens the gland appears lobulated on the dorsal surface while the convex ventral surface is devoid of the lobes. The glands appeared greyish in material preserved in 10 per cent. formalin. Surrounding the gland there is a network of blood vessels.

*Histology.* This gland consists of large spherical or oval vesicles held together by connective tissue. The vesicles contain colloid material and are lined by cubical epithelial cells with distinct nuclei. The tissue lying in between the vesicles is of the fibrous variety and contains here and there a blood vessel. It is interesting to note that in the intervacular tissue are also found groups of cells which seem to resemble the cells of the thymus gland. The cells of the vesicle and those simulating cells of the thymus contain granules. The gland is very richly supplied with blood vessels.



## THE HYOID APPARATUS (Fig. 10).

The hyoid apparatus presents some peculiarities in its shape, and its processes. The os hyoideum consists of a very thick cartilaginous plate, from which processes are given off and which forms the attachment to several muscles. The following parts may be distinguished in it.

*The body.* The body is broader than it is long. From the anterior end the anterior cornua take their origin and project from the anterior part of the body first towards the cephalic region and then curve backwards and upwards. The posterior cornua are bony rods which run from the hinder margin of the hyoid plate and enclose the laryngeal apparatus in the angle so formed. The cornua are ossified to a large extent and bear at their posterior ends caps of cartilage. The general shape of the posterior cornua differs from that of other Anura.

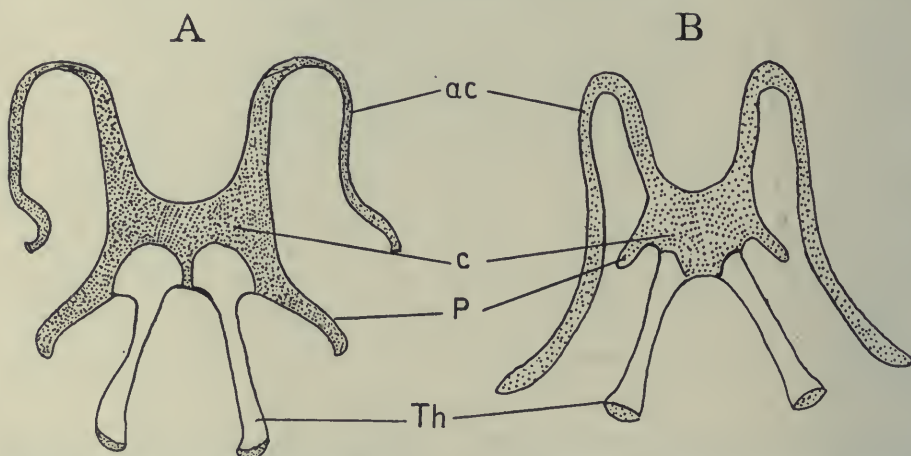


Fig. 10. A. Hyoid apparatus of *Ceratophrys*; B. Hyoid apparatus of *Hyla ewingii* (after Parker).  
Ac, anterior cornua, C, body of the hyoid, P, posterior cornua, Th, thyroid process.

It should be noted, however, that the hyoid apparatus of *Ceratophrys* differs from that of other Anura in several interesting details, the nearest approach to it being made by that of *Hyla ewingii* figured and described by Prof. W. K. Parker in his monograph on the development of the skull of the Amphibia.

The chief points of difference between the hyoid apparatus of *Ceratophrys*, and that of other Anura are:

- (1) The general shape and configuration of body cartilage.

The measurements are as follows:

Greatest length, 1 cm.

Greatest breadth, 1.8 cms.

Length of thyroid cornua, 2.5 cms.

Length of posterior process, 1.2 cms.

Distance between the ends of posterior processes, 3.2 cms.

Distance between thyroid cornua, 1.4 cms.

(2) In *Rana esculenta* and many other Anura from the anterior angle, there projects on either side, a blunt rounded process. The body plate of Ceratophrys is devoid of these processes.

(3) In *Rana esculenta* and allied forms the cornua styloidea bear anteriorly a process just at the point where it changes its direction. This process is unrepresented in the hyoid apparatus of Ceratophrys.

(4) The cartilaginous body plate has slight traces of ossification at the postero-lateral regions.

#### SUMMARY.

1. A description of the heart of Ceratophrys is given and variation in the position of the origin of a. oesophagea and a. subclavius is noted.

2. A detailed description of the conus arteriosus and of the valves in it is given.

3. The function of the valves in the conus arteriosus is discussed at length and the conclusion that at no stage a complete partition of the conus arteriosus into right and left cavities by the spiral valve coming close to the wall of the conus arteriosus is arrived at—a conclusion contrary to the views of Ecker, Gaupp and their followers.

4. The structure of the lung is studied. Attention is called to the remarkable development of muscular trabeculae.

5. The structure of the parathyroid gland and thyroid gland is described.

6. The peculiarities presented by the hyoid apparatus are noted.

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# THE OCCURRENCE OF POLYOVULAR GRAAFIAN FOLLICLES

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IN the large literature on the histology of the ovary there are occasional references to the occurrence of polyovular Graafian follicles, and in almost every case this is characterised as a rare phenomenon. In the examination of a series of ovaries for another purpose, this condition was met with in a relatively large number of specimens, which are described here.

Previously polyovular follicles have been recorded in human subjects by Schottländer(1), Nagel(2), Stoeckel(3), Rabl(4), Arnold(5); in bats by van Beneden(6); in cats by Rabl(4) and Schrön(7); in dogs by Waldeyer(16), Bouin(8), Wagener(9) and Smyth(10), in rabbits by Wagener(9) and Honore(11); in *Dasyurus* by O'Donoghue(12); in pigs by Corner(13), and Schmaltz(14); and in guinea-pigs by Loeb(15).

Unfortunately complete serial sections were not available in any of my cases, and the notes which follow refer only to one slide in each case.

*Dog 74* was an animal of about eleven months. The ovary contained several large follicles almost ripe, and many of middle size, but relatively few primordial follicles. In places the latter were crowded together to the point of slight deformation but none were polyovular. Of the middle sized and large ones, eight were counted with two ova, two with three, one with four and one with five ova. It is possible that serial sections would have revealed more. Fig. 1 shows the follicle containing five ova, and is particularly noteworthy in that one of the ova is separated from the others by a membrana propria, in the corner of which a few connective tissue cells may be seen. The ovary was otherwise normal except that the connective tissue was not conspicuous.

*Dog S.* This ovary contained two large corpora lutea, several half ripe follicles, and very few primordial follicles only one of which was biovular; six of the larger ones, however, were biovular and three triovular. One of the latter is reproduced in Fig. 2. At one side of the follicle is an old convoluted corpus luteum scar. The theca is not so well marked as is usual in dog's ovaries. One middle-sized follicle in another part of the section lies beside a large follicle, separated from it only by the membrana propria, and causing it to bulge inwards to a slight extent. This will be referred to later. This ovary contains more connective tissue than the preceding but still less than is normal.

*Cat Th.* This cat had been thyroidectomised fourteen days before it was killed. There were six large follicles one of which contained two ova, at opposite



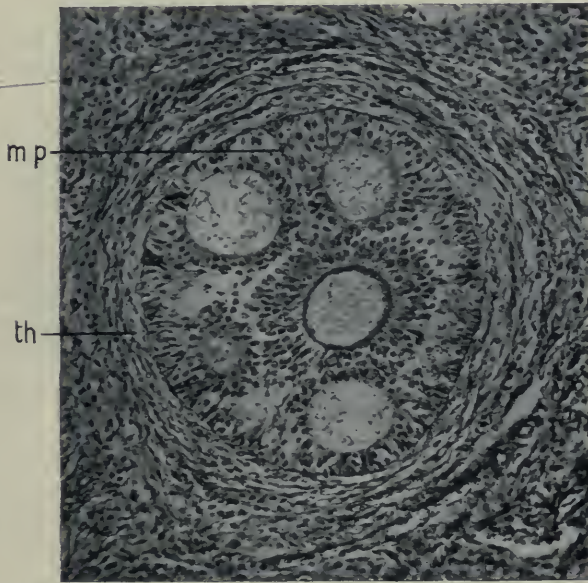


Fig. 1. Polyovular follicle of Dog 74,  $\times 50$ . The theca interna (*th.*) is well marked and one ovum is separated from the others by a membrana propria (*m.p.*).

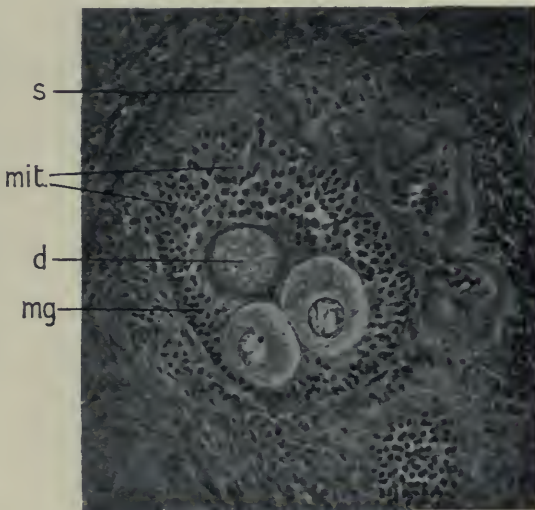


Fig. 2. Triovular follicle of Dog 5,  $\times 50$ . A convoluted corpus luteum scar (*s.*) lies at one side and several mitotic figures (*mit.*) can be seen in the membrana granulosa (*m.g.*). Notice the degenerating ovum (*d.*).

poles, and a large number of primordial follicles, of which at least 15 per cent. were double. Their appearance was similar to that in Figs. 4 and 5.

*Cat nn.* There were a large number of follicles of all stages present in the ovary and one fairly old corpus luteum with a flattened appearance; the stroma was highly fibrotic but the appearance was otherwise normal. Four large follicles were biovular, three triovular and one (Fig. 3) contained five ova, and was peculiarly flattened on one side. Many of the primordial follicles were biovular, having apparently been pressed, or grown into each other. None showed any signs of mitosis (Fig. 4).

*Rabbit A.* The section showed only a few middle sized follicles, but many primordial ones. In several places just below the germinal epithelium two primordial follicles had grown together so that the ova were immediately contiguous. No signs of division were observed in any of the cases (Fig. 5).

*Rabbit 19.* This animal had received some injections of corpus luteum substance. The ovary contained a large number of follicles, in all stages up to that of almost full ripeness, and no corpora lutea. Four of the follicles were biovular. The membrana granulosa of most of the larger follicles shows an interesting condition; some of the cells are arranged so that circular spaces are left, and these appear to be filled with liquor folliculi. These can be seen in Fig. 6 (c.s.) and to a less degree in Fig. 7, and are the "bodies" of Call and Exner.

One of the biovular follicles (Fig. 6) contained one ovum apparently normal and another markedly deformed. Under a higher power the cytoplasm of the former was seen to be granular with a few indistinct vacuoles in the centre, while the latter was very vacuolated. Another biovular follicle is shown in Fig. 7. Mitotic figures can be seen in the membrana granulosa cells.

*Rabbit 0.5.* The ovary contained very many follicles, mostly small, but was otherwise normal. The animal was about six months old. One large biovular follicle was found (Fig. 8).

*Rabbit nn.* The connective tissue of the ovary was not conspicuous, and a triovular follicle was observed wedged between two large follicles. The ova were large with well marked zonae pellucidae but the cytoplasm was degenerated.

*Guinea-pig nn.* A large corpus luteum occupied the main bulk of the ovary. There was one large follicle, and it contained two ova of unequal size, at opposite poles. There were only a few primordial follicles.

*Fowl nn.* In this case one follicle contained two closely apposed ova. The section was in other respects normal.

Several suggestions have been put forward regarding the mode of origin of this polyovular condition. Stoeckel(3) suggested that they arose from the division of a single cell body with two or more nuclei formed by amitotic division. The evidence is not strong and this suggestion has not found favour with later writers. Waldeyer(16) was of the opinion that mitotic division of the original oocyte was the cause of polyovulation. Schottländer(1) held that they arise either from the division of the primordial ovum, or the inclusion of

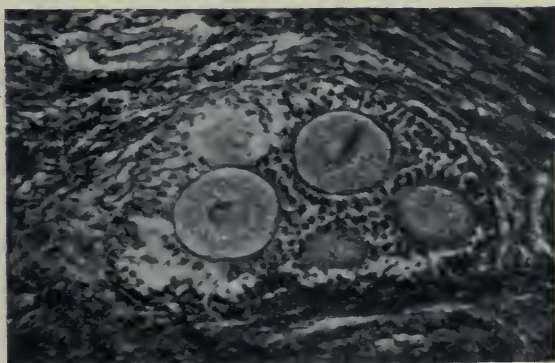


Fig. 3. Polyovular follicle of Cat *nn*,  $\times 50$ . The dense nature of the connective tissue can be well seen.

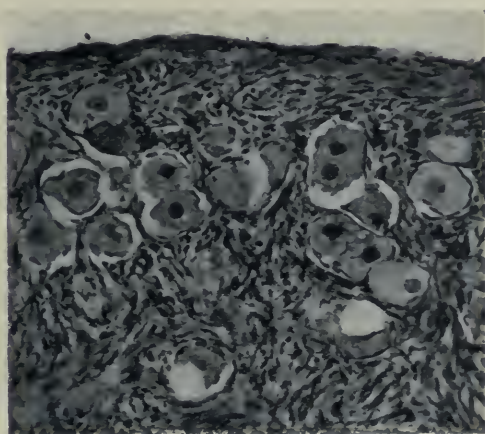


Fig. 4. Biovular primordial follicle of Cat *nn*,  $\times 180$ .

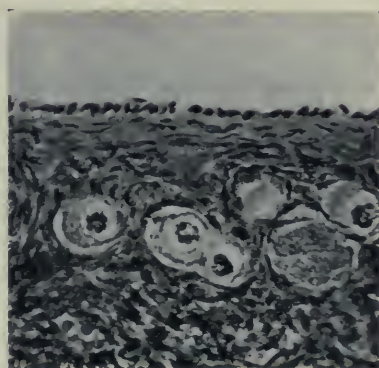


Fig. 5. Biovular primordial follicle of Rabbit *A*,  $\times 180$ .



two separate primordial follicles, and that the latter is the more probable. In this he is supported by P. and M. Bouin (8), Honore (11) and O'Donoghue (12). The last named author points out that if a large number of ova are present within the follicle, it is unlikely that there would be no indication of division stages in the remaining follicles, and moreover, the fact that the ova are frequently in different stages of development, militates against the theory of division. Arnold's interesting case of a woman whose ovaries showed 88 large polyovular follicles, containing up to thirteen ova, leads him to the conclusion that theories of division are not applicable to his material, but the probability is that the polyovulation is due to the development of a common follicular epithelium about two or more oocytes (5). In the present cases this seems to be the explanation in the majority, at least, though it is not quite clear whether it is due to a break down of connective tissue follicular cells or to the close contiguity of the oocytes from the earliest stages. Loeb (15) believes that the latter accounts for the origin of some polyovular follicles, but that the majority of cases are due to the intrusion of very small follicles, especially primordial follicles, into large ones. This also appears to be the explanation in some of those here, for in several cases, e.g. in Dog *S*, I have observed a small follicle pushed, as it were, through the theca of a larger one, and only separated from it by the membrana propria; indeed, in Fig. 1 one of the ova within the follicle is separated from the remainder by a membrana propria, to which some connective tissue cells still adhere. In no case was any evidence of mitotic division found. Loeb observed the polyovulation in the hypotypical ovary of a thyroidectomised guinea-pig and suggests that both modes of origin are due to the same cause, namely, relative inactivity of the connective tissue. Unfortunately only two case histories were available to me, viz. Cat *Th* and Rabbit 19, and both had been subjected to conditions calculated to bring about an hypotypical condition of the ovaries. However, several of the other specimens are somewhat hypotypical, and certainly indicate that Loeb's explanation has a strong foundation.

Arnold (5) suggests that the smaller of the oocytes in a follicle containing several, might be arrested in development and probably degenerate so that all might disappear save one; or else that all might undergo atresia and never reach the stage of extrusion of the ovum. Schmaltz (14) is also of this opinion.

Several of the figures show a degenerative appearance in one or more of the ova, particularly Figs. 2 and 3, which is very probably brought about by the increased competition for nourishment.

Corner (13) suggests that a few cases of migration of the ovum may be accounted for by polyovular follicles; but the liquor folliculi does not appear to be formed in any quantity in very many of these follicles, although it is amply present in a few, and this would lessen the chances of the ovum entering the tube, according to Broman (17).

Smyth (10) reports a case of two pups from a litter of fourteen, which had several polyovular follicles in their ovaries, one follicle containing seven ova.



Fig. 6. Biovular follicle of Rabbit 19,  $\times 50$ . One ovum (*d.*) is markedly deformed in shape and circular spaces (*c.s.*) are seen in the granulosa. The theca interna is very well marked.

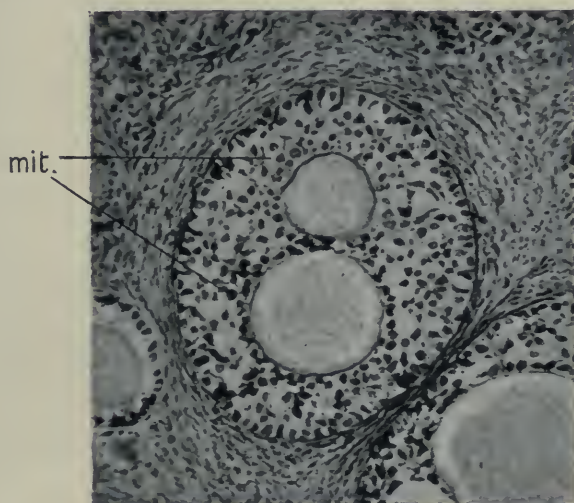
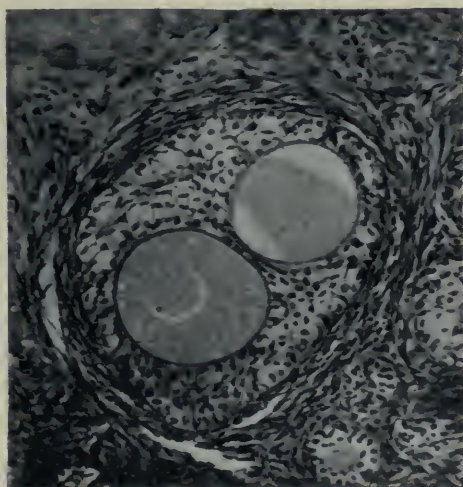


Fig. 7. Biovular follicle of Rabbit 19,  $\times 50$ .



Another of the pups had a litter of nine at the first birth. He considers this interesting as pointing a possible correlation between polyovulation and high fertility, but this appears to be not quite justified.

#### CONCLUSIONS.

Polyovular follicles are not of extremely rare occurrence and may be associated with a hypotypical ovarian condition. The mode of origin is probably partly due to primordial follicles becoming enclosed within the same theca, and partly to the intrusion of a small follicle into a large one.

The expenses of this research have been defrayed by the Earl of Moray Fund of the University of Edinburgh.

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# AN HERMAPHRODITE DOGFISH (*SCYLIORHINUS CANICULA*)

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THE dogfish described in this paper was found among a number from Plymouth dissected by students in the Department of Zoology and Comparative Anatomy; University Museum, Oxford in 1919. Fortunately the student had only opened the abdominal cavity when the abnormality was noticed and the specimen preserved.

External observation sufficed to show that the animal was abnormal. There were two claspers (Fig. 1). The right one was nearly as large as that of

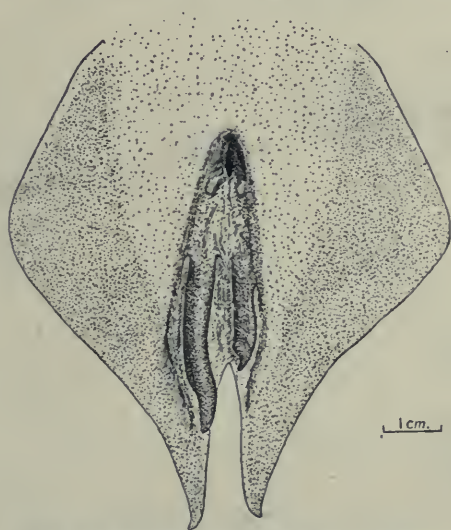


Fig. 1. The claspers and pelvic fins of the hermaphrodite.

a normal male. The left on the other hand was smaller and somewhat deformed. The pelvic fins were separated from one another posteriorly as much as in a normal female. In a normal male they are joined together almost to the tip.

On dissection it was found that there was a normal and apparently functional ovary, in which eggs were found up to a volume of about 2 c.c. To this were attached two pieces of tissue which on microscopical examination proved

to be testes. The larger of the two pieces of testis was only 3 cms. long; the other was much smaller. They were attached to the same fold of peritoneum as the ovary, with which the smaller lay in very close relation (Fig. 2). The

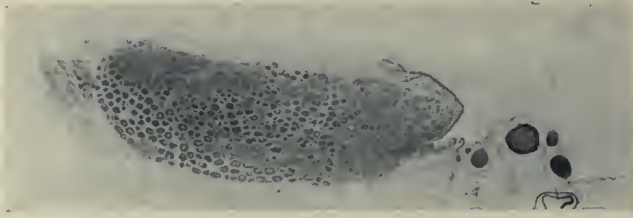


Fig. 2. Section through the ovary and attached testis.

demarcation of the testes was sharp, there being no transitional tissue. Histologically, the testis tissue appeared normal with all stages in spermatogenesis up to fully formed spermatozoa (Fig. 3). On one side of the larger

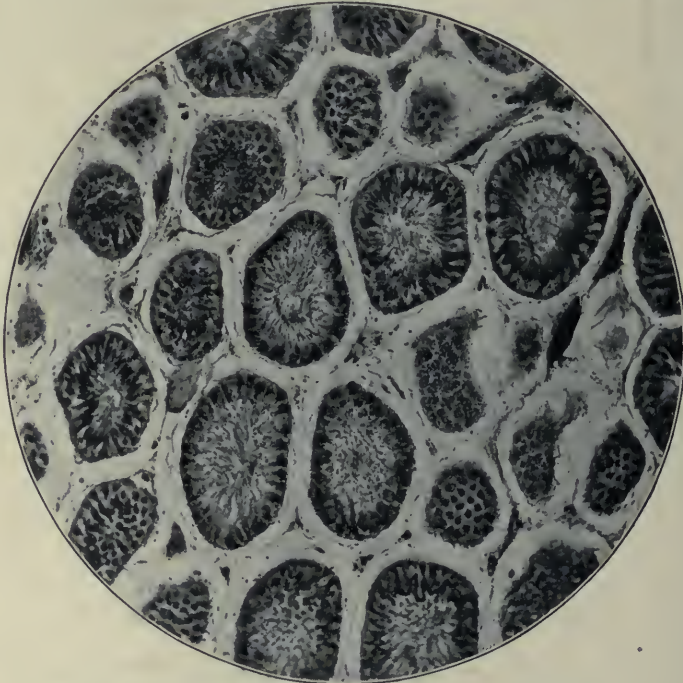


Fig. 3. Section through the testis, more highly magnified.

testis there were a number of tubules which probably constituted the rete testis. No trace of vasa efferentia was found.

Both oviducts were normal, with shell glands, etc., of the usual size.

The anterior part of the mesonephros approached the male condition in being better developed than in the average female. The Wolffian duct in its

anterior region shewed a condition intermediate between those of the two sexes. In the normal male it is a thick very much coiled tube, functioning as the vas deferens. In section (Fig. 4a) it is seen to be ridged internally, and its epithelium (Fig. 5a) consists of a single layer of ciliated cells with peculiar secretory cells scattered among them. In the normal female, on the other hand, the Wolffian duct follows a straight and narrow path leading to the urinary sinus. It is much smaller than the homologous duct in the male (Fig. 4b), and it is not thrown into folds internally. Its epithelium is two layered and not ciliated (Fig. 5b). In the hermaphrodite the duct is intermediate in thickness between the male and female condition (Fig. 4c), and it is somewhat sinuous. It is thrown into folds internally as in the male, but its epithelium is of several layers (Fig. 5c) and not ciliated, and does not contain any of the peculiar secreting cells characteristic of the male.

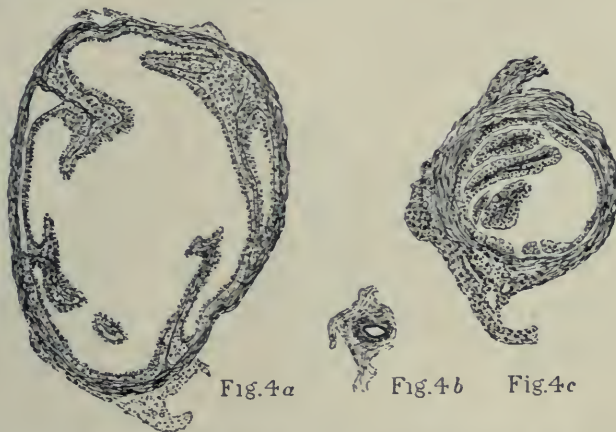


Fig. 4. Sections through the Wolffian duct (all three drawings at the same magnification). a, a normal male; b, a normal female; c, the hermaphrodite.

The posterior part of the Wolffian duct in the male is differentiated into the vesicula seminalis, in the female into the urinary sinus. Both the vesicula seminalis and the urinary sinus of normal specimens are considerably larger than the corresponding region of the Wolffian duct of this hermaphrodite. The vesicula seminalis of a normal male is similar histologically to the more anterior region of the same duct, which has just been described. The urinary sinus of the normal female has an epithelium similar to that of the female Wolffian duct further forward, but beneath this lie a corium, a layer of circular muscle fibres, a layer of diagonal muscle fibres, and a layer of longitudinal muscle fibres, in the order named. The corresponding part of the Wolffian duct in the hermaphrodite resembles the female condition except in the far less orderly arrangement of muscle and connective tissue.

The arrangement of the ducts leading from the posterior region of the mesonephros of the hermaphrodite to the exterior was of the normal female type. A further female character was the absence of any sign of a sperm sac.



## DISCUSSION.

Hermaphrodites in Elasmobranchs are excessively rare, only two previous cases being known to the writers. One of these was described by Hock (3). This was a specimen of *Raja clavata*, the bad preservation of which rendered detailed description impossible. A complete set of functional female organs, ovary and ducts, was present, and in addition, on the left side, there was a testis with ripe spermatozoa and a clasper.

The other case was described by Vayssi re and Quintaret (4). On the left side there was no clasper and a complete set of female organs was present, differing only from the normal in that the shell gland was ill-formed and of three times the normal length. There was a well-developed ovary with a testis attached to its free edge. On the right side there was a clasper, and a complete set of male organs. There was also a normal oviduct present on this side.

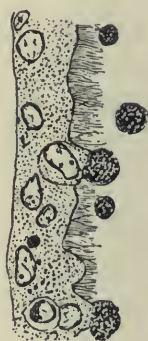


Fig. 5a



Fig. 5b

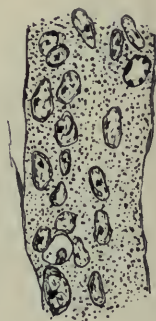


Fig. 5c

Fig. 5. Sections through the epithelium of the Wolffian duct (all three drawings at the same magnification). In all three drawings the lumen of the duct is to the right. *a*, a normal male (the Wolffian duct is here the vas deferens); *b*, a normal female; *c*, the hermaphrodite.

The following may be advanced as a very tentative hypothesis which would cover many of the facts.

The individuals are supposed to be bilateral gynandromorphs, in which gynandromorphism has been over-shadowed by the sex-hormones in a varying degree. This is the same hypothesis as that put forward by Bond (1) to account for his hermaphrodite pheasant; but in Bond's case the gynandromorphism was less obscured. According to this theory, the side that is male in its chromosomes responds more readily to the testicular hormone, while the side that is female responds more readily to the ovarian hormone. Put in another way, the theory is that when both testicular and ovarian secretions are circulating in the blood and are balancing one another, a slight difference in the tissue itself may be sufficient to cause maleness or femaleness in any part of the body. The difference in the tissue concerned may be chromosomal, or it may be of a metabolic nature. The latter explanation must apply to the tail

feathers of Bond's pheasant, for the outer half of each feather was male and the inner half female.

It is to be noted that the writers' case shows its gynandromorphism only in the poor development of the left clasper, and probably would not have been described as a gynandromorph had not the only other known cases of hermaphroditism in Elasmobranchs been of this nature.

The differences between the three cases are perhaps to be accounted for on the additional assumption that the testicular hormone began to act at different times relative to the ovarian hormone in the three cases. Possibly the organs cannot be readily modified by sex-hormones except at a certain definite time in development. Thus the writers suppose that the left clasper in the case here described was developed to some extent because the testis commenced its secretion sufficiently early, whereas in the other two cases one of the two claspers was not developed at all because the testis commenced its secretion too late to modify towards maleness a part which was female in its chromosome constitution. This time-factor hypothesis is similar to that adduced by Dr F. A. E. Crew<sup>(2)</sup> to account for differences in the degree of intersexuality in intersexual pigs and goats. Different relative amounts of testicular and ovarian hormone would also have different effects.

The writers fully realise that their hypotheses do not cover all the facts. They wish to express their obligations to Prof. E. S. Goodrich and to Mr H. M. Carleton for anatomical and histological advice, and to Mr J. S. Huxley for valuable criticism of the hypothetical part of the paper.

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## BILATERAL EPIPHYSIS AT THE BASAL END OF THE SECOND METACARPAL

By CECIL P. G. WAKELEY, F.R.C.S. (ENG.)

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THE occasional appearance of an additional epiphysis at the base of a metacarpal or of a metatarsal bone other than the first is of interest morphologically, surgically, and also from the standpoint of the radiologist.

The following case of a basal epiphysis of the second metacarpal in both hands occurred in a female child aged two years. The only other child in the family was a girl aged four years whose epiphyses, as ascertained by skiagrams, were normal for that age.

The ossific centres of the heads of the four inner metacarpals are well developed while that for the basal end of the first metacarpal is only just indicated in the skiagram. The only carpal bones which showed any sign of ossification were the os magnum and unciform. The epiphysis for the distal end of the radius is present while that for the head of the ulna has not yet appeared.

In both hands the basal part of the second metacarpal appears to be separated from the shaft by a well-marked constriction. The ossific centre for the basal epiphysis of the first phalanx of each of the four inner digits is well marked, and is just indicated in the proximal phalanx of the thumb on the left side. The ossific centres of the epiphyses for the bases of the second phalanges of the first, second and third fingers were present but those for the little fingers had not yet appeared. The nucleus for the epiphysis of the distal phalanx was present in the thumb and second finger only.

It may be worth while recapitulating the various theories which have been put forward in explanation of the peculiarities and ossification of the first metacarpal and metatarsal bones and the reduction in the phalanges in the thumb and great toe.

Since the time of Galen in the second century, the difference between the thumb and the remaining digits has attracted the interest of anatomists and surgeons; and, on account of the resemblance in the ossification of the first metacarpal bone to that of a true phalanx and the absence of one phalanx in the thumb and great toe, it was considered that the metacarpal and metatarsal bones of the thumb and great toe represented morphologically the first phalanx.

Gegenbaur, however, contested the prevailing theory and brought forward evidence to show that the metacarpal bone of the thumb was in reality a true metacarpal bone and that the same evidence applied to the metatarsal



bone of the great toe. The principal evidence which was brought forward in favour of Gegenbaur's theory was concerned with the relations of the muscles of the thumb and great toe; the occasional presence of a distal epiphysis in the first metacarpal or metatarsal bone and in the fact that the apparent exceptions to the rule that the epiphysis of the first metacarpal in certain of the mammalia such as the rabbit were in reality due to an error in the numbering of the digits in these animals. In the rabbit what is apparently the first metacarpal or metatarsal bone is proved on closer examination to be the second; a rudimentary first metatarsal being developed in embryonic life and



Fig. 1.

being easily visible in the foot of a young rabbit during the first month of extrauterine life. In the adult animal, however, this rudiment together with the first cuneiform fuses with the base of the second metatarsal and appears merely as a projecting tubercle on its inner aspect.

If one considers the musculature, one is struck with the large development of the muscles of the ball of the thumb in the adult as compared with those of the first phalanges of the other fingers in which on the dorsal aspect there is only the aponeurosis of the tendons of the extensor communis digitorum muscle into which are inserted, with the exception of the fifth finger on the dorsal side, the corresponding lumbrical muscles and on the palmar aspect, the interossei muscles. As regards comparative anatomy the developmental

history of the human subject shows a gradual evolution of the thumb musculature by a differentiation of the radially situated interossei muscles which has led to the characteristic capability of opposition of the human thumb.

Welcker emphasizes the importance of the origin of the first dorsal interosseus muscle, the insertion of the opponens pollicis muscle and other muscles of the thumb as evidence of the metacarpal nature of the first metacarpal bone. The extensor "longus and brevis" pollicis muscles are originally separated bundles of the extensor communis digitorum muscle. The extensor longus pollicis muscle must be regarded as a radially disposed slip of the extensor communis digitorum muscle to the distal phalanx of the thumb, and the extensor brevis pollicis as an ulnar slip of the same muscle. The tendon of the extensor longus pollicis muscle passes to the dorsal surface of the second phalanx of the thumb, and is situated on the ulnar side of the long axis of this phalanx. It represents on the ulnar side of the thumb the terminal portion of the most radially placed tendon of insertion of the extensor communis digitorum muscle into the third phalanx of a finger.

The tendon of the extensor longus pollicis muscle is reinforced by a thin tendinous slip from the ulnar side of the extensor brevis pollicis muscle which is blended with the tendon of the extensor longus pollicis muscle and represents the middle slip of a tendon of the extensor communis digitorum muscle into the second phalanx. Given off from the radial border of the tendon of the extensor brevis pollicis muscle, is a still stronger bundle corresponding to the radial slip of the lateral insertion of the extensor communis digitorum muscle into the third phalanx of a finger. The expanded principal insertion of the tendon of the extensor brevis pollicis muscle thus corresponds with the middle slip and tendon of insertion of the latter muscle. This part which courses over the long axis of the first phalanx of the thumb is not inserted into the base or the dorsal surface of the first phalanx as one would expect if the metacarpal of the thumb in the greater part of its extent represented a first phalanx—but it goes beyond the joint to the dorsal-surface of the base of the second phalanx—indicating that the third phalanx of the thumb has absorbed the original second phalanx, the two being represented by a single enlarged phalanx bearing the nail.

With regard to the palmar aspect of the thumb, Fürst pointed out that the strong bundle known as the Fasciculus Exilis which springs from the flexor sublimis digitorum muscle and joins the long flexor of the thumb represents the flexor sublimis pollicis muscle which would like the proper tendons of the flexor sublimis digitorum muscle be inserted into the second phalanx of the thumb. The long thin tendon of the fasciculus is inserted along with the tendon of the flexor longus pollicis muscle into the distal phalanx which has assimilated an element which in the other fingers is represented by the second phalanx.

Thomson has also discussed the position of the first metacarpal and first metatarsal bones and confirmed Schwegel's theory that frequently in the

thumb traces of a distal, and in the remaining digits, traces of a proximal epiphysis are found, and that these have fused with the shaft at an earlier period of development.

Uffleemann attempted to unite the two opposed theories and prove that the first "middle hand" and "middle foot" bones were neither true "middle hand" or "foot" bones nor first phalanges, but could be explained as a representative of both. According to Uffleemann at a certain stage of development which lasts for a period of several years, there is an appearance of a special bony nucleus in the head of the first metacarpal, although in reality such a nucleus is never really present. In the new-born infant the distal cartilaginous epiphysis is somewhat less extended in the distal direction than the proximal epiphysis. In the remaining metacarpals it presents an annular constriction. The proximal epiphysis appears in the third year and fuses with the diaphysis in the sixteenth year, which is an earlier date than any other epiphysis of the hand bones. Between the end of the first and third year after birth, a stump-like process from the lower or distal end of the diaphysis grows into the cartilaginous epiphysis which on the radial side remains widely separated from the surface of the cartilage; on the ulnar side, however, it does not reach the surface. In the eighth year the diaphysis projects by means of this process nearly to the articular surface. On the radial side there remains between this process and the corresponding part of the extremity of the diaphysis a thin layer of cartilage which is for a long time excluded from the articulation. This layer at the twelfth year is 0.7 mm. thick. Sections therefore which pass somewhat to the radial side of the longitudinal axis of the bone, afford at this period the picture of an independent nucleus, while further ulnarwards the bony substance of the shaft and head are continuous. At the twelfth year the intervening cartilaginous disc gradually ossifies from the deeper part towards the surface. Before ossification is completed, the macerated bone shows a more or less deep groove on the radial side between the head and middle piece, which might be regarded as indicating an incompletely fused epiphyseal border.

The condition of nutrient foramina in the bones of the thumb was studied by Humphry and W. Krause. While in the first phalanges of the four inner fingers the nutrient foramina are situated near the distal end of the proximal third of the bone and are all directed distally. In the first metacarpal the nutrient foramen is directed distally and somewhat to the ulnar side. The nutrient foramina of the second, third, fourth and fifth metacarpals are situated near the radial border of the volar surface of the shaft, and lead to a proximally directed canal. In this character the first metacarpal does not conform to the arrangement in the other metacarpal bones but corresponds with that of the phalanges. The condition of the nutrient arteries and their canals indicate that the growth of the bones at a certain embryonic period is relatively less rapid than that of the blood vessels and soft parts, for the nutrient arteries become proximally directed.



Pfitzner also attempted to explain the two segments of the thumb by a coalescence of two bony rudiments. He believed that the large distal phalanx of the thumb and great toe had assimilated the second phalanx and become indistinguishably fused with it. Soon after Pfitzner had propounded his assimilation theory, Salzer published the case of a man with three phalanges in both thumbs; and this man's sister had a thumb with two phalanges, the distal phalanx was exceptionally long and a constriction was present in the centre of the bone, an indication that fusion of two phalanges might have taken place.

Salzer agreed completely with Pfitzner in considering the last phalanx of the thumb as homologous with the second and third phalanges.

Reider came to the same conclusion by studying the case of a man with three segments in the thumb; and this man's four children all had the same deformity.

Fürst at a later date agreed with Pfitzner's assimilation hypothesis on account of the study of a hand in a man with a three jointed thumb.

Pfitzner himself at a later date described two cases in which there were three phalanges to the thumb on each side; thus he was able to demonstrate his hypothesis which he had propounded some years before.

With regard to comparative anatomy, W. Krause is of the opinion that no explanation is to be expected because the thumb is more highly developed in the human subject than in any other species of the whole animal kingdom. Even in the apes the thumb is rudimentary. However, on the other hand Thomson points out that in some animals, for instance the kangaroo, koala and elephant, there is a much more complete and regular formation of a distal epiphysis in the metacarpal and metatarsal bones than in the higher mammalia, constituting in them what is apparently the normal mode of ossification. Further the peculiar condition observed in the seal in the forefoot of which animal the ossification follows the usual plan, while in the hind foot distal epiphyses are fully developed in the first metatarsal bone and in all the phalanges except the terminal. Moreover in *Ornithorhynchus* there is a tendency towards the formation of both distal and proximal epiphyses in all the metacarpal bones, and, finally in the Cetacea the fullest extension of these accessory points of ossification is met with, proximal and distal epiphyses being present in all the metacarpal bones and all the phalanges except the less developed distal series.

It may not be out of place to give an historical survey of the various theories which have led up to the present conception of the morphology of the metacarpal and metatarsal bones of the hand and foot.

1. First metacarpal and metatarsal bones regarded as the basal phalanx of the thumb and toe on account of the proximal position of the epiphysis and the presence of only two segments in the thumb and great toe. (Galen.)
2. The position and direction of the nutrient canals in the first metacarpal and metatarsal bones are similar to that of a phalanx. (Krause and Humphry)

3. First metacarpal and metatarsal bones are the true middle hand and middle foot bones. (Gegenbaur.)
  - (a) Gegenbaur's view supported by the homologies of the associated muscles. (Weleker and others.)
  - (b) The occasional presence of distal epiphyses in the first metacarpal and metatarsal bones; and the confirmation of these observations in the human subject by the presence as the normal condition of true epiphyses at both ends of the metacarpal and metatarsal and proximal series of phalanges. (Thomson and Schwegel.)
  - (c) Occasional presence of three phalanges in the thumb and great toe. (Salzer and others.)
  - (d) Critical examination of pseudo-epiphyses at the bases of the second metacarpal and metatarsal bones. (Michaelis and Von Wyss.)
4. First metacarpal represents the true metacarpal which appears as the proximal epiphysis and in addition the first phalanx which forms the shaft and distal end. (Uffleemann.)
5. Occasional epiphyses at distal ends of the first metacarpal and metatarsal and at the bases of metacarpals and metatarsals 2 to 5 are false or pseudo-epiphyses. (Freund.)
6. Accessory carpal bones which may be mistaken for true basal epiphyses of the second or third metacarpals and form one type of pseudo-epiphysis.
  - (a) Parastyloid.
  - (b) Trapezoides secundarium. (Pfitzner.)
7. Distal phalanx of thumb and great toe represents the fused second and third phalanges. Assimilation hypothesis. (Pfitzner.)

In conclusion the balance of evidence seems to be in favour of Gegenbaur's original assumption, that the first metacarpal and metatarsal bones are true middle hand and middle foot bones, and Pfitzner's theory that the two phalanges of the thumb may be explained as resulting from the fusion of the middle with the distal phalanx is apparently correct.

My thanks are due to my colleague Dr R. J. Gladstone for his help and suggestions which he has put at my disposal in writing this article.

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## JOINTS

### THE LIMITATION OF THEIR RANGE OF MOVEMENT, AND AN EXPLANATION OF CERTAIN SURGICAL CONDITIONS

BY E. JOYCE PARTRIDGE, F.R.C.S.

WHY does not energetic muscular activity normally endanger Joints? This is a question which has always seemed to me to be answered inadequately by the theories of movement and limitations of movement of joints as generally put forward by anatomists and physiologists; and it was in seeking a more satisfactory answer to this question, and in finding an anatomical fact with a functional value, that an explanation of this as well as certain pathological surgical conditions seemed to present itself.

Some of the conditions referred to are the adduction of the femur in tubercular disease of the hip, the dislocation of joints which occurs in certain muscular paralyses, the so-called "congenital" dislocation of the hip, and the sudden disorganisation of joints in Charcot's disease.

These four pathological states will be referred to later; let us return for the moment to the normal joint. Consider first the weight of a limb when amputated, and the range and force of movement carried out in every limb by young and healthy subjects; when one thinks of these things and considers also the extreme disadvantage in regard to leverage at which the ligaments of all joints act, can one say that the strength of their ligaments is sufficient, even when supplemented by the support of the muscles surrounding them, always to protect joint ligaments from rupture or even joints from dislocation?

The physiologist may give one reply to these questions by saying that normal muscular tone protects joints: and he is undoubtedly correct, because, by reason of its "tone" mechanically stretched muscle tends mechanically to contract, so that extension of a limb causes increased tension of the flexors and these therefore tend to contract and so prevent dislocation of their joint by hyperextension. Indeed, to carry this one step further, it has been proved that it is only by the reciprocal innervation of muscles, whereby the contraction of one group sends an impulse of relaxation to the opposing group, that movement is ever possible, or that the animal body escapes being muscle bound.

In this connection also it is interesting to remember the extreme flail-like condition of a limb in a case of flaccid paralysis; one has the feeling on moving such a limb that a very little excess of zeal in examining the range of movement in the joints, might cause dislocation in any of them; and from this one may deduce two things: That the ligaments do not limit the range of movement in



a normal healthy limb, and that even in a voluntarily relaxed limb the muscles check any excessive range of movement at the joints.

This physiological protection of joints does not seem to me, however, to be an adequate explanation of the freedom from accident of the animal joint in every case. Consider for example the violent extension that takes place at the knee in kicking an object such as a football, or better still, the more violent extension caused by an attempt to kick the object and failure to strike it; in such a case the heavy leg and foot swinging forward at the knee joint are moving with considerable momentum. What happens? The swing is, of course, checked as soon as possible by the higher centres; but such intervention is relatively slow, and it is very doubtful whether the message would generally arrive in time to protect the joint. Let us suppose therefore that the normal reflex contraction associated with muscle tone shortens the flexors and stops hyperextension. This would protect the joint it is true; but in the case of the knee joint the flexors, besides crossing this joint, cross also either the hip or the ankle. Here therefore a weak point in this physiological protection of joints emerges, for if the reflex contraction which we know occurs, does so when the muscle is stretched to the point of danger to the joint, it cannot account for the protection of either joint when the muscle crosses two joints. In the case of the hamstrings acting on the knee therefore, in order to allow sufficient length of muscle to admit of normal extension at the knee with the hip flexed, it should become possible with the hip extended to hyperextend the knee without any intervention from muscle tone, similarly with the *gastrocnemii*.

This protection of joints by muscle tone fails therefore for the knee joint, and it becomes probable that it is not the true explanation of the protection of joints generally.

On the strength of these considerations I was first led into an investigation of the whole subject and found to my mind a much more satisfactory explanation of the relative immunity of joints from dislocation in the well developed nerve supply to all moveable joints, and the association of this nerve supply with the nerve supply to the muscles moving those joints.

This association is, of course, expressed in Hilton's Law<sup>1</sup> thus:

"The same trunks of nerves whose branches supply the groups of muscles moving a joint furnish also a distribution of nerves to the skin over the insertion of the same muscles; and the interior of the joint receives its nerves from the same source."

But although this law is still quoted by teachers of anatomy as a fact of a certain value to the labouring anatomical student, since Hilton's time a real appreciation by the surgeon of the value of his words seems to have disappeared.

With regard to the cutaneous distribution of nerves which Hilton mentions, that is to my mind of less importance than the muscular, although it has its own value, but with regard to the relationship of the innervation of muscles

<sup>1</sup> *Rest and Pain* (1887) by John Hilton, F.R.S., F.R.C.S., Lect. VII.

and joints, that bears further investigation and I hope to show later has a bearing on the study of more than one surgical condition found in joints.

Let us therefore reconsider Hilton's Law, and to begin with let us elaborate it thus:

No joint is moved by any muscle whose nerve does not also supply a twig to that joint, and all the nerves which supply a moveable joint are branches of the nerves which supply the muscles moving the joint, and their distribution is on that surface of the joint which is controlled by those muscles.

Here, however, let us hastily add, lest there be misunderstanding: the above statement can easily be proved correct in relation to *all* joints except those of the shoulder girdle and hip, in which case the joints being so near the great limb plexuses, their nerve supply comes in some cases, not from the same named nerve as that which supplies the muscles which move them, but from the same nerve trunk or trunks. This fact is difficult to embody in a precise law but forms no real exception to the rule.

In this restatement of Hilton's Law I say no joint is *moved* by any muscle whose nerve does not also supply a twig to that joint; and here I say *moved* with a purpose because in joints with little or no movement this rule does not apply.

Thus in the sacro iliac, an almost immobile joint supported by perhaps a larger ligamentous mass than any other joint in the human body, the nerve supply is so negligible as to be entirely omitted from nearly all text-books of anatomy. Why? Because being an immobile joint there is no need for any relationship between the joint and the muscles crossing it, since the former cannot be influenced by the latter.

The next point in our restatement of Hilton's Law is that *every* muscle that moves a joint is related by nerve supply to the joint which it moves. Hilton says vaguely in effect that the interior of the joint receives its nerve supply from the same source as the groups of muscles moving a joint, and this is perfectly true; but it is also true that if an isolated muscle from a group crosses a joint not acted on by the group as a whole, that isolated muscle becomes related to the foreign joint by its nerve supply although the joint may have apparently an adequate supply corresponding with the muscles acting on it in groups. An example will make this clearer, thus: In the case of the gracilis muscle which crosses the knee joint, this muscle belongs to the group of adductors of the thigh; and is supplied together with the adductors by the obturator nerve; but because this muscle is inserted distal to the knee joint the obturator nerve sends a twig to that joint, and this, in spite of the fact that the knee joint is already well supplied with nerves and the main distribution of the obturator nerve is in the upper part of the thigh, so that to reach the knee a long slender twig has to be sent out to some distance from the principal ramifications of the parent nerve.

The next point in the restatement of Hilton's Law is that "all the nerves which supply a moveable joint are branches of the nerves which



supply the muscles moving the joint." This is merely the converse of the previous statement; but it has its own importance in adding weight to the argument. Thus in the case of the elbow joint, all the deep nerves crossing it give twigs of supply to the joint because they all supply muscles acting on the joint; this is not remarkable owing to their relatively close relationship to the joint, but the musculo cutaneous nerve which is becoming superficial above the elbow and not an immediate relation of the joint, also gives a supply to the joint, whilst the internal cutaneous, which is about the same size, and similarly situated, does not; the reason for this being found, of course, in the supply of the musculo cutaneous to the biceps and brachialis anticus which act on the joint, whilst the internal cutaneous is purely a cutaneous nerve.

To continue investigating the restated law it appears that the nerves supplying joints do so on that surface of the joint which is controlled by the muscles receiving the same supply. Thus in hinged joints the nerve supplying the flexor or extensor muscles is generally found lying on the corresponding surface of the joint, and may for that reason supply it on that surface; but in the case of a ball and socket joint such as the hip, to find the obturator nerve which supplies the adductors going to the lower and inner surface of the joint, to find the twig from the anterior crural which goes to the flexors supplying the anterior and antero-superior surface of the joint, and the twig from the sciatic which corresponds with the supply to the extensors going to the posterior and posterosuperior surface, is to my mind worth consideration, especially when the other great enarthrodial joint, the shoulder joint, shows equally well the same arrangement.

In view of the above anatomical facts it seems probable that there is some functional relationship between muscles acting on joints, their nerve supply and the branch that nerve gives to the joint. Abduction of the thigh, for example, may be carried on, not till the great trochanter touches the acetabular margin as we are sometimes told, but until the capsule on the mesial surface of the joint, on reaching a certain degree of tension, issues a message to the adductors to contract. Extension at the knee goes on not until mechanically stopped by the post-capsular ligament and the anterior cruciate ligament, but until the tension in them is sufficient to issue a reflex message to the flexors of the knee to contract, and so on throughout the body.

The above is the part played by the capsule and capsular ligaments, but there is no doubt that muscle tendons where they cross joints and become attached to bone close to the articular extremities, also share the responsibility of protecting joints.

It was well established by Professor Henry Head<sup>1</sup> that deep pressure sense, and sense of passive position, may be conveyed from structures such as joints by branches from the motor nerves running down the tendons to the neighbourhood of joints; but Professor Stopford<sup>2</sup> also proved that passive sense of

<sup>1</sup> *Studies in Neurology*, vol. I, ch. VIII.

<sup>2</sup> J. S. B. Stopford. "The nerve supply of the interphalangeal and metacarpophalangeal joints." *Journ. Anat.* Oct. 1921.



position in joints may also arise from the nerve supply to the joints not associated with the nerves of the tendons. The value of the nerves which reach a joint by running in the tendon is apparently twofold; some of them on reaching the neighbourhood of a joint leave the tendon, and supply the surrounding structure, and act in a manner similar to the ordinary nerve supply to the ligaments, capsule, etc., whilst others end in ramifications in the tendon itself. This double distribution indicates a double function; those which leave the tendon and end in the structures surrounding the joint are said to bear Pacinian corpuscles, and they undoubtedly function as nerves of deep pressure sense and carry the stimuli which indicate joint position; that is to say, they convey information indicating which part of the capsule and surrounding structures are stretched, and which are lax, thus giving the higher centres information of the position of the various members, but also protecting the articulations from misuse by over-stretching any particular ligament or part of the capsule. Dr F. W. Mott<sup>1</sup> states: "I believe this sense of position of joints is due to a complex group of sensations arising in alterations in tension of structures about joints rather than in the alterations of contact of surfaces...in judging the sense of position in limbs."

The nerves on the other hand which end in ramification in tendon, serve the same purpose of protecting the joint, but they probably act in a slightly different manner, and they are probably responsible for the well-known phenomena of "tendon reflexes." Here, instead of the overstretched ligament or capsule issuing a reflex message for the muscles to contract and avoid mishap, the tendon of the muscle itself, crossing the joint close to, or amalgamated with the capsule, is fully supplied with nerves. A sudden stretching of the tendon announces that in a moment, unless the muscle is prepared, it may be too late in contracting to save the capsule on that surface from also being stretched; in other words a sudden stretching of the tendon heralds danger to the associated joint; and it is because of this danger that the reflex contraction of the muscles occurs. A simple experiment in this connection will serve to illustrate the value of the protective mechanism in the tendons.

Rest the elbow on the arm of a chair or some convenient support, with the forearm held comfortably vertical midway between pronation and supination, and the hand swinging loosely at the wrist. Now sharply fling the forearm laterally by a rotation of the upper arm outwards, so that the loosely swaying hand is flung backwards: The hand seems as it were to bounce, the recoil of the flexor muscles and tendons preventing hyperextension, but there is no reflex contraction of these muscles drawing or holding the hand forwards, and it just drops back with perhaps another one or two bounces if the movement has been performed sufficiently sharply. Now continue the experiment by sharply rotating the upper arm inwards; the bounce does not occur, but on the contrary the hand is pulled sharply back and held there by the extensors, and does not drop forwards again. The explanation is simple: The extensor

<sup>1</sup> D'Arcy Power and J. Keogh Murphy. *A System of Syphilis*, vol. IV, p. 361.

tendons are longer than the flexors, and extension at the wrist much more limited than flexion, so that whereas it is inconceivable that by flicking the hand backwards the joint might be endangered, it is easily possible to imagine the reverse happening, flinging the hand forwards with sufficient force might cause a forward dislocation, also the posterior part of the capsule of the wrist is not much strengthened by ligaments, consequently the tendons are called upon for protection; the sudden stretch of the tendons across the back of the joint when the hand is jerked forwards causes a reflex contraction of their muscles, pulling up the hand and preventing the joint injury which might otherwise occur.

This action is similar to a tendon-reflex elsewhere, and has to my mind the same significance, and if it were possible to swing or flick any other of the joints at which tendon-reflexes are ordinarily elicited, the same effect would, I believe, follow!

A physiological explanation of the course taken by the nerve impulse is outside the scope of this paper; indeed, I do not wish to do more than point out that it is significant that all joints have a full nervous protection associated so closely with the movements produced in them that it is an invariable rule that the same nerve which causes a certain movement in any joint bears also a sensory twig from the joint, announcing surely the extent to which that movement has been carried. And the fact that it is the same nerve which carries the sensory stimulus and the motor impulse suggests a very simple reflex with perhaps a single cell-station at the nearest possible point to the nerve distribution.

In connection with the reflex protection of joints the process of mastication is interesting. Here it is not only the joint which may suffer through excessive activity on the part of the masticatory muscles, but the teeth and all the structures adjacent to them might also be damaged. In a limb injuries which might conceivably be caused by excessive muscular activity are limited to injuries to the bones or joints; whereas in the case of the mandible, excessive muscular activity might also break the teeth or bite a piece out of the tongue or cheek. That such an accident does not occur must be due to the fact that all the structures in danger, together with the muscles of mastication, are supplied by the 5th nerve, and a similar reflex to that mentioned above comes into action; otherwise it is marvellous to consider in biting any thin hard object (such, for example, as a ginger biscuit) that at the moment when the biscuit breaks, the teeth do not meet with sufficient impact to crack their enamel! Again, in the continuous use which is made by man of speech and mastication, when the tongue and cheek are constantly applied to the inner and outer side of the teeth, it is surprising that the accident of biting them does not more often occur. Everyone knows how painful, but how infrequent such an accident is; but does anyone know a sane person who has ever by voluntary muscular activity accidentally bitten a piece right out of either their tongue or cheek? And is it not probable that this accident is prevented by the fact that all these structures, together with the muscles which open the



mouth<sup>1</sup> are supplied as already stated by the 5th nerve, and the rapid reflex already mentioned is called into action.

In movements at this joint it is possible that the nerve supply to the capsule of the joint is one of the most important factors in supplying the afferent side of this reflex. Indeed, a simple experiment would seem to demonstrate that when the teeth are closely approximated the capsule, or part of it, is tense: thus in most people in the ordinary position of rest, although the mouth is shut the teeth are not closely approximated; but on propping up the chin with the hand for one or two minutes so that the teeth are pressed together, although the masticatory muscles are relaxed, a distinct feeling of discomfort is felt in the neighbourhood of the joint, and the mouth is opened when the pressure is relaxed, with a sense of relief, showing surely that the capsule of the joint is so arranged that in order completely to close the mouth the posterior part of the capsule must be slightly stretched, enough, at any rate, to give a stimulus heralding the dangerous proximity of the upper and lower teeth.

To return once more to Hilton's Law. He states that "The same trunks of nerves whose branches supply the groups of muscles moving a joint, furnish also a distribution of nerves to the skin over the insertion of the same muscles." This is, broadly speaking, true; but not so invariably and literally exact as in the case of the nerve supplying a muscle or group of muscles and its joint.

Hilton<sup>2</sup>, for example, cites a relationship between the anterior crural nerve supplying the sartorius muscle of the thigh and the internal saphenous branch of this nerve with its cutaneous distribution, by saying that the muscle is inserted in the fascia of the inner side of the leg, and that the fascia spreads down to the inner side of the foot, whilst the nerve supplies the skin over this area of fascia. This is, I think, a little far-fetched; but it does not for that reason negative the fact that there is a relationship between the nerve supply to muscles and skin in many cases; in fact, broadly speaking, all over the body

<sup>1</sup> In connection with mastication, it should be noted that the movement of opening the mouth is incorrectly described in many anatomical text-books. It is said to be caused by gravity, the mylohyoid, the geniohyoid, etc., with assistance from the external pterygoid, drawing the condyle forward. This description can readily be proved incorrect by opening the mouth against pressure, and at the same time performing the act of swallowing, when it will be found that the hyoid moves up and down in the usual way, thus eliminating hyoid muscles as active depressors. Moreover, the power to open the mouth against pressure is so great that it is impossible to hold shut the mouth of a person determined to open it, and it is therefore obvious that some powerful muscles are opening the mouth, and muscles, we have just proved, which are not associated with the hyoid bone. The muscles in question must be the external pterygoids of the two sides, the temporal, masseter, and internal pterygoid muscles being readily discounted by feeling them act during the process of raising the mandible against pressure. The external pterygoid unfortunately cannot be felt, but the process of opening the mouth consists of causing the mandible to rotate about its axis of rotation, so that when the condyles glide forwards on to the eminentia articularis, the horizontal ramus must be depressed. Now the fibres of the external pterygoid passing as they do horizontally backwards from the zygomatic fossa to the neck of the mandible and capsule of the joint, must on contraction draw the condyles forward, and the axis of rotation being fixed by the opposing action of the masseters and internal pterygoids of the two sides, drawing the condyles forward, causes depression of the horizontal ramus.

<sup>2</sup> *Rest and Pain*, Hilton, *ch. ix.* p. 214.



this law holds good, and where it does hold good, it seems to me that the relationship is probably similar to that already described for the muscles and joints—i.e. the distribution to the skin is related to that of the muscles in order to help in controlling the action of the muscles. Stretching the skin, for example, over the extensor surface of a joint, joins with the other afferent stimuli in restraining excessive muscular activity, and skin contact on the adductor surface reflexly prevents waste of energy in pressing neighbouring surfaces together.

In conclusion: The same nerve which supplies any muscle supplies also the structures which are affected by movement of that muscle. In effect, muscular activity throughout the body is controlled by afferent stimuli from all the connective tissue structures either stretched, compressed, or in any way affected by that activity; the connection between the afferent and efferent stimuli being close, and the reflex a quick one.

The foregoing anatomical facts and their functional significance, have at least a possible relationship to a number of pathological conditions which merit further investigation. Paralytic dislocations of joints, for example, are certainly elucidated; because in paralytic dislocation one or more of the muscles in relation to a joint are paralysed, and consequently protection of the joint by reflex contraction of those muscles is lost.

Adduction of the thigh in tubercular disease of the hip may also be explained, for if all muscular activity is controlled by afferent impulses sent out from connective tissue, when it is subjected to stretching, compression, etc., it seems probable that disease in the head of the femur, by irritation of the obturator nerve, may cause an irritative contraction in the adductors which this nerve also supplies. It being significant in this connection that the stage of the disease in which adduction occurs is often said to correspond to the stage of the disease in which the head of the femur is suffering invasion.

Congenital dislocation of the hip also is a phenomenon hitherto not fully explained, which these anatomical conclusions may be said to elucidate.

This deformity is by many surgeons no longer thought to be truly congenital in the sense that it occurs at or before birth, but rather at the time when the limb is first extended to support the weight of the infant. If this is the case the deformity which always occurs by a slipping out of the head of the femur on the lateral surface of the joint, may by the foregoing anatomical conclusions be explained; for a weakness of abduction of the joint at the time when the limb is brought down into the extended position must occur. The gluteus medius and minimus, the main abductors in the adult, are, in the flexed limbs of the infant, solely rotators; and it is easy to imagine therefore that when the limb is first extended they may upon occasion be slow to take up their new rôle of reflex abduction, thus leaving the joint unprotected on its abductor surface, and any slight hyperadduction is uncorrected, so that after a time the capsule on the lateral surface of the joint becomes much stretched and the head of the femur rides out of the acetabulum.

Finally Charcot's joints are undoubtedly explained by pathological conditions influencing the nerves, the anatomical distribution of which has previously been described. Disease of the central nervous system leads to loss of the sensory side of the reflex arc for joint protection, and this again to repeated assaults upon the joint by over-stretching in various directions of the capsule and ligaments; and the subsequent synovitis, disorganisation, and frequent dislocation of the joint is the inevitable result.

Indeed Charcot's disease is in a way strong evidence in favour of the presence of the reflex protection described for all moveable joints. Charcot's disease is what would happen to all our joints if we had to depend for their safety on the strength of their bony contour, their capsule, their ligaments, and the support of their surrounding muscles, instead of on the reflex protection afforded by the extensive sensory nerve supply which all moveable joints possess, and the muscles supplied by the same nerves.

#### SUMMARY.

Ligaments would more often suffer strain were they the only protectors of joints from dislocation, and normal muscles are not so arranged that their tone is adequate to protect joints from injury in ordinary circumstances.

There is, however, a very close relationship between the nerve supply to muscles crossing a joint and the joint itself, suggesting a closer functional relationship between them than is usually appreciated. This relationship is only manifested for moveable joints, these being the only ones in danger of dislocation by excessive muscular activity; and muscles supplied by a nerve are always connected by the supply of that nerve to the particular surface of the joint on which those muscles act, again emphasising the functional relationship between the two structures. Tendons also carry branches from the motor nerve supplying their muscles to the structures surrounding their insertions, and to the neighbouring joint surface, these branches being proved to be sensory.

Thus joints are by their nerve supply very closely linked to the muscles which act on them and this anatomical fact has a probable functional value.

The constant nerve relationship suggests a simple reflex arc protecting joints by reflex muscular contraction, both from simple strain caused by excessive muscular activity, as well as from more violent injury.

In cases where structures other than the joint are in danger from excessive muscular activity (such, for example, as the teeth, tongue, etc., in relation to the process of mastication) it is found that the reflex protection holds good for all the structures involved, all being supplied by the same nerve. Skin also, in relation to joints, can give information of the extent of movement taking place in the joint and is supplied by the same nerve as the muscle causing the movement. Thus all muscular activity throughout the body is controlled by sensory stimuli from all the structures affected by that muscular activity.

Certain pathological conditions are elucidated by the foregoing anatomical facts, notably adduction of the thigh in tubercular disease of the hip, congenital dislocation of the hip, and Charcot's disease of joints.

## HERMAPHRODITISM IN A MOLE WITH MALE EXTERNAL GENITALS

BY KATHARINE ROUNSFELL BROWN,

*From the Institute of Physiology, Glasgow University.*

THE occurrence of a mixed sex gland in mammals is sufficiently rare to warrant this record of a case, although several instances of such hermaphroditism have been recorded.

Krediet (1, 2) described the occurrence of an ovo-testis in a goat with female genitalia, but marked male characters of head and sexual behaviour. And in a later paper he describes a case, also with female secondary characters, in which the left gonad was a testis and the right an ovo-testis.

Sand (3) recorded the case of a boy (?) in whom the presence of gonads, on the right an ovary, and on the left an ovo-testis, were determined.

Crew (4, 5, 6, 7) has recently published notes of several cases in domestic animals, frogs and fowls. In those instances where there were definitely mixed sex glands, the noteworthy point has been that the animal had developed the sex characters relating to the gland whose functional tissues were the more predominant; in nearly every case this was a testis. Also, as a rule, the testicular tissue showed signs of activity, mitosis being present, and often spermatogenesis. More especially was this marked in animals with male external genitalia.

The ovo-testis to be described occurred in a mole with male external genitalia, killed in October, 1920, and forming one of a series used by Mr Watson (8) in the study of the suprarenals during the oestrous cycle. The intestines had been removed and the animal skinned and preserved before reaching the laboratory, so that more detailed examination was impossible. The animal was small, and sections of the tibial epiphyses were made, in an attempt to ascertain the age of the animal. As they were ossified it may be concluded that the animal was not a young one.

The penis was well developed and normal to naked eye inspection, the prostatic swelling was present, though small. There was no sign of a vaginal orifice, or of any female internal genitalia. The apparent testes lay in the abdominal cavity, outside the pelvis, and they were attached to the posterior abdominal wall by a mesentery containing blood vessels. The connections with the genito-urinary system had been destroyed in removing the organs. No seminal vesicles were found.

Behind the bladder and opening into the urethra posteriorly were the remains of a tube, present also in the normal animal, but differing slightly microscopically. The mucous membrane lining both was thrown into folds.



In the hermaphrodite these were covered by columnar epithelium not present in the normal mole. The scent glands in the flanks of this animal were less prominent than in the normal adult mole, and there were no scrotal pouches. The gonads were the normal size noted for testes during October.

In each the ovarian tissue formed a crescentic strip applied to one side of the organ. On the right side it formed one-sixth of the circumference with breadth .19 mm., the diameter of the whole gland being 4.25 mm. On this side the ovarian portion did not extend to either pole. On the left side it formed one quarter of the circumference; the diameter of the gland was 3.7 mm. and that of the ovarian part .59 mm. Here the ovarian tissue formed

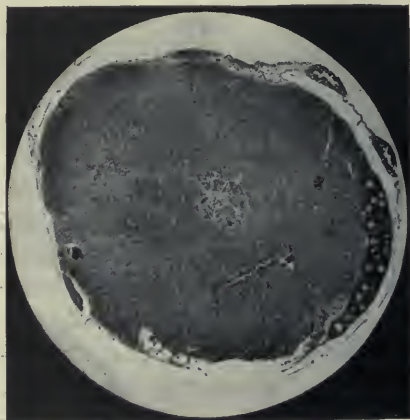


Fig. 1.

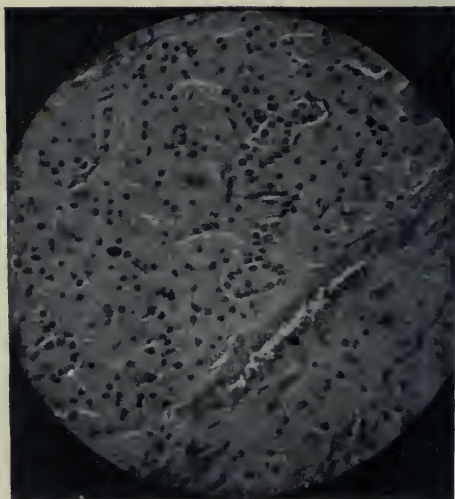


Fig. 2.

one pole of the organ, and isolated follicles appeared among the cells of the testicular part (fig. 1).

On the right side the oval organ was composed of densely packed cells, except in the centre where the tissue was rarified. The ovarian portion was covered by germinal epithelium, and was composed of Graafian follicles in early stages of development, embedded in a spindle-celled stroma (fig. 3).

The main mass of the organ had a fibrous tissue capsule, and was composed of two types of cells, the *A* type being large pale-staining cells with granular cytoplasm and large oval nuclei. These cells were distributed in groups of six to ten, best seen in the more rarified central portion. They had the appearance and to some extent the arrangement of tubular cells, but neither basement membrane nor lumen was present in any group (fig. 2).

The *B* type of cells were also large, with less granular cytoplasm, and smaller dark-staining nuclei. These cells formed the bulk of the section, and they closely resembled normal interstitial cells.

In sections stained for fats by Sudan III and also by Nile Blue Sulphate the *A* type of cells did not take up the stain, whereas those of the *B* type showed a marked lipoid content. In a control section taken from a normal male killed at the same time, the tubular cells did not stain, but the interstitial cells show a staining reaction equal to that of the *B* cells.

The line of separation between the two portions was definite, and in it were several large blood-vessels.

Lying alongside the ovarian portion was a tube, oval in transverse section, whose appearance suggested that it was a Fallopian tube, but its ultimate destination was unknown (fig. 4). Against the opposite side of the same organ lay another tube, composed of a single layer of cubical cells with spindle-shaped

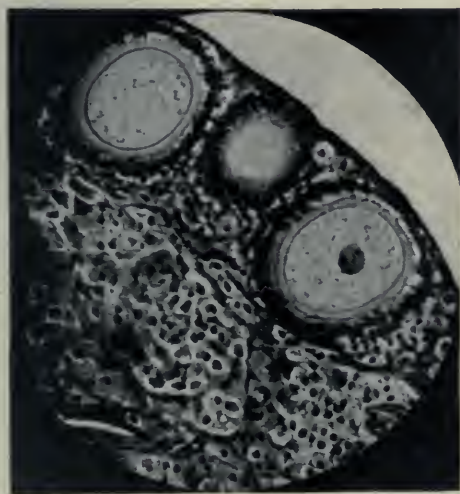


Fig. 3.

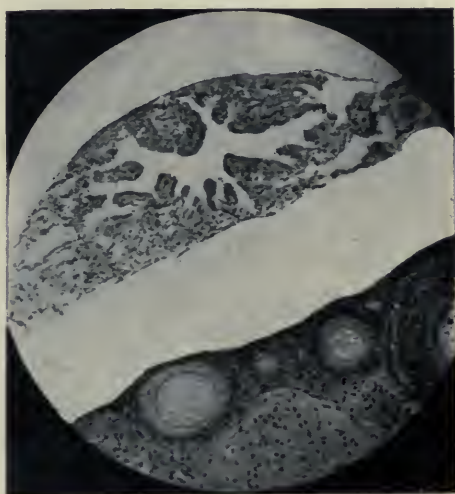


Fig. 4.

nuclei. This tube was like the inner coat of a vas deferens, lacking its muscular wall.

The left organ was round and smaller than the right one; as in the other, the ovarian portion was covered by germinal epithelium, and contained many immature follicles. The testicular part contained both *A* and *B* types of cells, but here the *A* cells were less numerous and more scattered, and there was very little evidence of any attempt at tubule formation.

On this side the line of demarcation contained some fibrous tissue in addition to blood vessels. No accompanying tubes were found.

The interesting feature of this case is that the mole was to all appearances masculine, although somewhat small, while the testicular part of the gland was non-developed, as far as the tubules were concerned. The ovarian portion, on the other hand, was composed of healthy, normal-looking follicles.

All investigations, from the early observations of Shattock and Seligman,

show that it is the interstitial cells of the testis that constitute the puberty gland, and determine the development of male secondary characters. In this animal these cells were well developed and formed a mass far in excess of the ovarian part of the gland. To this may be ascribed the development of the male secondary sexual characters.

I thank Professor Noël Paton and Mr Watson for the encouragement and help they have given me in the carrying out of this work.

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# A CASE OF POLYDACTYLIA SHEWING CERTAIN ATAVISTIC CHARACTERS

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AND

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THE specimen which we are about to describe is the right foot of an adult male Egyptian. The left leg had been amputated, and no history as to the condition of the left foot could be obtained. The brothers and the sisters of the person concerned were free from any abnormality.



Fig. 1. Dorsal aspect of the foot.

In fig. 1, which is a direct photograph from the dorsal aspect, is seen six digits, the first of which is directed inwards at a pronounced angle, similar to the thumb of the hand.

The longest toe is the third, and each toe has a nail.

The sole of the foot shews the skin thickened on the lateral border and on the ball, especially of the three lateral toes.

The X-ray photograph (fig. 2) shews that the skeleton of the foot consists of tarsus, metatarsus and phalanges. There may be seen the navicular, cuboid and second and third cuneiform bones, the talus and calcaneus having been removed.



Fig. 2. X-ray photograph of the foot.

A, digit representing the lateral division of the hallux. B, digit representing the mesial element of the divided hallux. Its base is united with the internal cuneiform.

The great toe consists of one bone, and it is impossible to separate its various parts.

The proximal extremity articulates with the navicular bone and also on its lateral side with the second cuneiform in its lower part.

The first cuneiform bone is apparently absent, but it is represented by the proximal extremity of the toe, the lines of junction with the metatarsal being well shewn in fig. 2.

The two other cuneiforms should be regarded as the second and third, for they articulate proximally with the navicular bone and distally with three toes in such manner that the second articulates with an additional toe to which it is fused and the normal second toe, while the third cuneiform articulates with the third normal toe.

Lateral to the third cuneiform is the cuboid, which articulates with the fourth and fifth toes in the normal manner.

All these articulations have been proved by dissection.

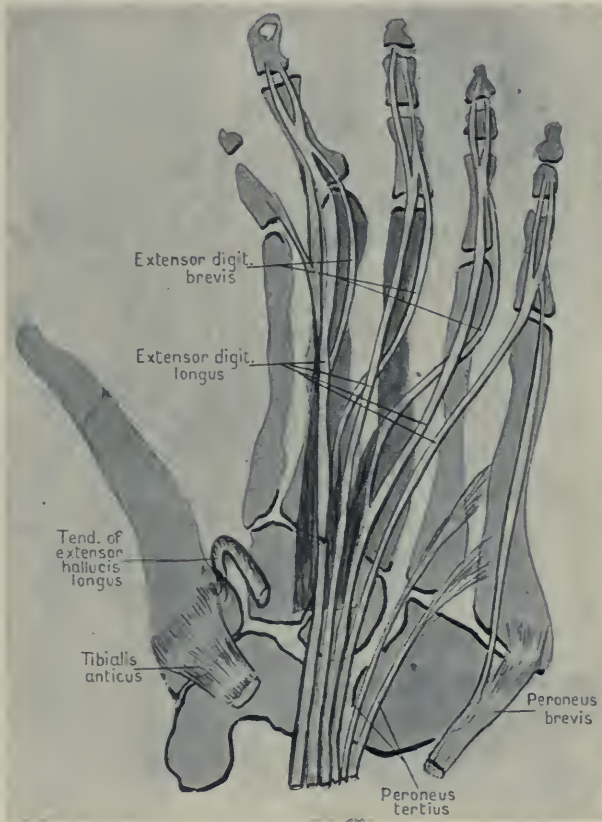


Fig. 3. Dissection of dorsum of the foot.

On dissection the muscles of the foot were found as follows:

*Dorsal aspect* (fig. 3). Extensor digitorum longus consists of four tendons which are directed to four toes from the third to the sixth, being attached to the second and distal phalanges.

To these tendons at the level of the first phalanx the extensor digitorum brevis sends an attachment. The first division of the extensor digitorum brevis sends two slips which are attached in the same manner as the above, but from



the medial slip an extra attachment goes to the first phalanx of the additional toe.

Lateral to the extensor digitorum longus is the peroneus tertius composed of two tendons which are inserted as fascial slips into the sixth metatarsal bone.

The tibialis anticus is inserted into the base of the first toe slightly distal to its articulation with the navicular bone.

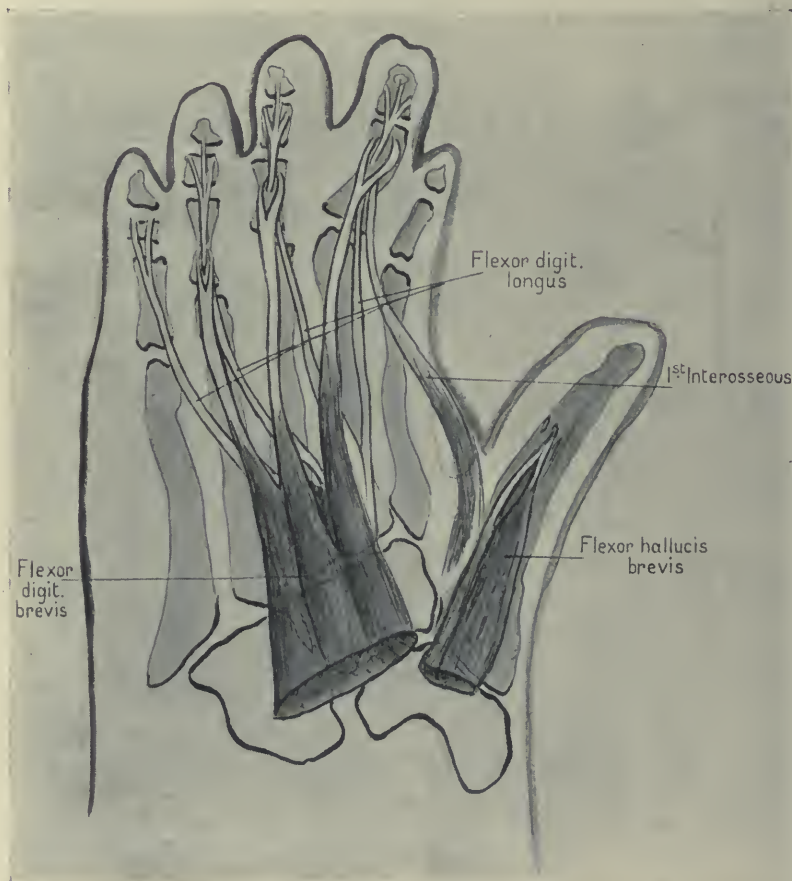


Fig. 4. Dissection of plantar aspect.

The peroneus brevis goes to the styloid process of the sixth metatarsal bone and sends a slender slip to the tendon of the digitorum longus in the manner of an extensor.

The short extensor of the great toe is absent.

The extensor hallucis longus is not inserted dorsally but passes between the great and additional toe to the plantar aspect where it will be subsequently described.

*Plantar aspect.* In the plantar aspect the following muscles are found (figs. 4 and 5):

*M. flexor digit brevis* sends tendons only to three toes, namely, to the third, fourth and fifth toes of this specimen, being inserted into the middle phalanx in the normal manner.

*M. flexor digit longus* with the lumbrical muscles is inserted into the third, fourth, fifth and sixth toes in the normal manner.

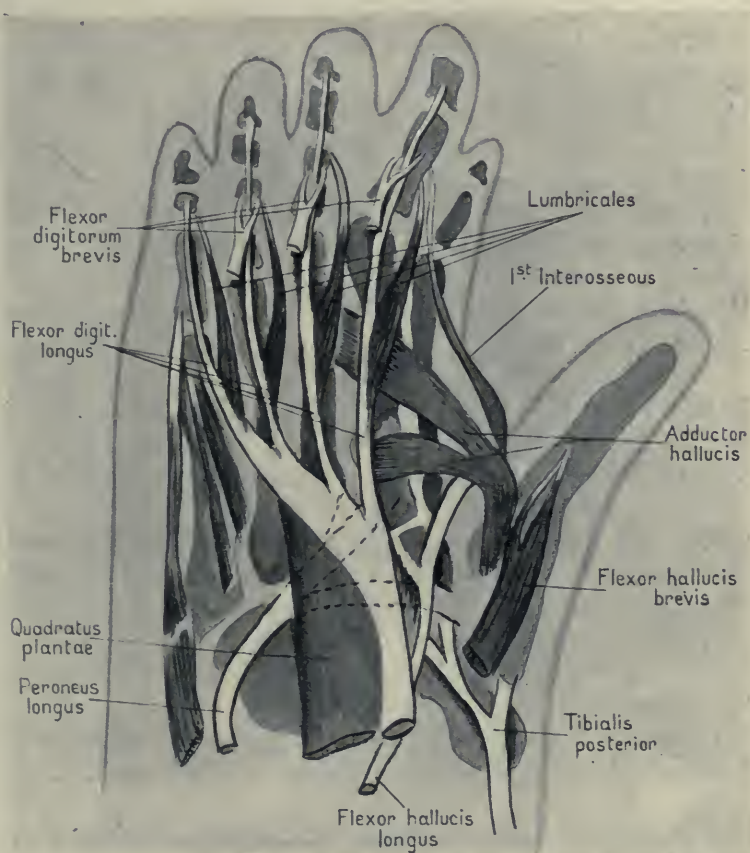


Fig. 5. Dissection of plantar aspect.

*M. quadratus planti* is present and inserted in the normal manner.

*M. flexor hallucis longus*, after crossing the flexor digitorum longus, gives to the latter a strong slip and continues to the dorsal aspect of the foot under the adductor hallucis, losing its original function.

The tibialis posticus, after insertion into the navicular bone and the base of the great toe, sends two strong slips to the second and third cuneiform bones.

In the lateral aspect of the foot, in the sulcus of the cuboid and under

the longitudinal plantar ligament is the peroneus longus muscle, which is inserted into the base of the great toe, the base of the third metatarsal and into the second and third cuneiforms.

The eminence of the great toe consists of a mass of muscle, possibly the abductor hallucis fused with the flexor brevis hallucis, both being inserted together at the site of the sesamoid bones.

The adductor hallucis has a direction which more resembles the adductor pollicis with oblique and transverse heads and is inserted into the base of the metatarsal bone of the great toe, or what we assume to be such. The eminence of the little toe consists of abductor, flexor and opponens muscles normally disposed.

The interosseous muscles are situated in such manner that, on the dorsal aspect, there are four muscles which represent abductors from the middle line which, in our specimen, passes through the *third* digit.

The first interosseous muscle is composed of two parts (fig. 6), one of which takes origin from the base of the great toe and the other from the third metatarsal, missing the additional toe.

On the plantar aspect there are three interosseous muscles attached in the usual manner to the fourth, fifth and sixth toes, being adductors to the middle line.

In the additional digit there is a tendinous slip without muscle passing from the base of the metatarsal to the first phalanx on its mesial aspect. Vessels and nerves are normal, but the dorsal artery of the foot gives off its deep plantar branch between the additional digit and the third metatarsal.

From the above dissection we suggest that the first toe represents the normal great toe, the second toe is an accessory toe and that the third, fourth, fifth and sixth toes represent the normal second, third, fourth and fifth toes. This is proved by the fact that the second toe, which we shall call the accessory toe, has no muscles attached to it and that all the muscles found which are normally attached to the great toe are attached to the first toe, the apparent absence of the first cuneiform being explained by the fusion of this bone with the first metatarsal, indicated by the articulation of the toe with the navicular bone.

The fourth, fifth and sixth metatarsals articulate normally with the third cuneiform and cuboid.

The second cuneiform articulates with or is ankylosed to the accessory toe and the third (or second normal) toe.

If the accessory toe be removed, then the rest of the skeleton of the foot is normal.

The arrangement of the muscles further bears out our suggestion, for the tendon of the tibialis anticus, which should be inserted into the medial aspect of the first cuneiform and first metatarsal, is inserted into the great toe in the position where the line of junction is indicated in the X-ray photograph and by the insertions of the tibialis posticus and peroneus longus.



The change of direction of the adductor hallucis may be explained by the changed position of the great toe which represents the thumb.

The arrangement of the interosseous muscles is a further proof that the second toe is accessory because the middle line of the foot passes through the third toe which is the longest and is apparently the normal second toe.



Fig. 6. Shewing arrangement of dorsal interosseous muscles.

If we now turn to the Simiidae, we find that in the gorilla the pedal interosseous muscles are grouped about the third digit in the majority of cases, and in a few cases about the second digit, the first arrangement corresponding to that in the chimpanzee, orang, some varieties of gibbon and the Cercopithecidae generally, the second corresponding to that found in man. In this respect the gorilla is in a transitional stage of evolution, and intermediate between the Hominidae and the other Simiidae (Duckworth, *Morphology and Anthropology*).

Our specimen would appear to lend support to the above statement, and the evolution from a six-toed ancestor with prehensile great toe, if such has

occurred, would seem to have had an intermediate step in which the second toe was suppressed, thus allowing the great toe to fall into line with the remaining four as in present day man.

The assumption that there was an extra digit between the great toe and the second toe is supported by certain described variations in the cuneiforms. Thus Dwight (*Anat. Anz.* vol. xx, p. 465) has described two instances of the

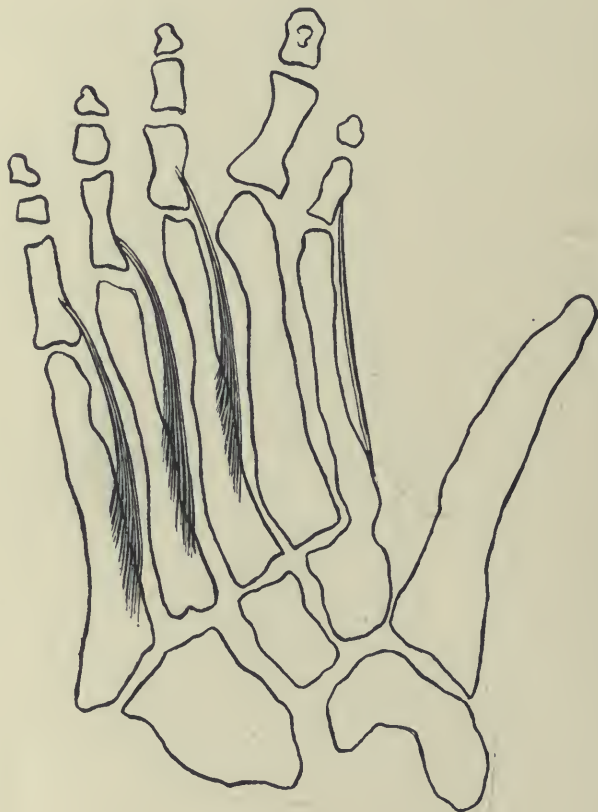


Fig. 7. Shewing arrangement of plantar interosseous muscles.

occurrence of an os intercuneiforme on the dorsum of the foot at the proximal end of the line of articulation between the internal and middle cuneiform bones.

Cunningham states that numerous cases of division of the internal cuneiform into dorsal and plantar parts have been recorded, and the frequent division of the metatarsal articular facet is no doubt correlated with this anomalous condition.

The constriction at the base of the metatarsal bone of the accessory digit in our specimen, as seen in fig. 2, might reasonably be assumed to be an extra

cuneiform bone, the persistence of which explains the condition found by Dwight.

We desire to express our thanks to Professor D. Derry for his help and criticism during the preparation of this note, and for his kindness in reading it.

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## SOME FEATURES OF THE ELBOW-JOINT

BY A. RALPH THOMPSON, CH.M., F.R.C.S.

THERE are some points in connection with the elbow-joint, which are worthy of attention and, perhaps, of explanation. These features are as follows:

- (1) The "carrying" angle.
- (2) The division of the joint into, at least, two parts.
- (3) The presence of an apophysis on the inner side of the trochlea of the humerus.
- (4) The limitation of flexion of the joint.

In addition, the reason of certain features in the radio-ulnar joint may be considered here:

(5) A well-marked area on the circumferential articular surface of the head of the radius, which is much deeper than the rest of the surface.

(6) The sacciform nature of the synovial cavity of the upper and lower radio-ulnar joints.

Certain other points may arise, but these do not require a separate heading.

(1) *The carrying angle.* This is the term which is applied to the angle which the forearm makes with the upper arm. It is open outwards, and has received attention in a paper written by H. Percy Potter in the *Journal of Anatomy and Physiology*, vol. xxix, pp. 488-491. The author states in this paper that the carrying angle is more pronounced in females than in males; and that there is no deviation inwards of the forearm across the upper arm during flexion of the joint. These statements, which Dr Potter makes, are definite and accurate. It is strange that they have not received the attention to which they are entitled, and, in fact, statements are still made in text-books that the forearm is carried across the upper arm in flexion of the elbow-joint, and the reason for this speculation is that the hand is thus carried more easily to the mouth for purposes of eating, than it otherwise would be. As if men had not moveable cervical vertebrae and a central nervous system.

A statement, which is diametrically opposed to this, has been made to the effect that the angle does disappear during the movement of flexion, and the following analogy is offered, in explanation of the supposed disappearance. If a piece of paper be cut with straight sides sloping away from each other, and, at their meeting points, the paper be folded across, the angle disappears when the sloping sides are folded over. This is quite a simple demonstration, but it does not hold good for the elbow-joint. That it is not analogous in any way may be easily demonstrated, by giving up mathematical speculation, and experimenting upon the joint itself. For this purpose it is necessary to move the humerus upon the ulna, and to note the disappearance of the angle, during flexion, and the cause of this disappearance. The experiment may be

performed as follows: a hole is bored through the humerus just above the lower end, and approximately through the axis of movement; a metal rod is fixed in the hole, and mounted on a suitable support, in such a way that the bone may be rotated easily. The ulna is then articulated with the humerus, and is kept in contact with it by means of a spring. The ulna need not again be touched. The humerus is so placed that it lies in a position of extension. The ulna now makes an angle with the humerus of about 170 degrees, opening outwards. The humerus is now brought through a movement of flexion, and it will be seen that the angle disappears, but that the bones do not cross each other, and, therefore, no "eating" angle is formed at all. The angle disappears because of the varying depth of the inner lip of the trochlea. The inner lip is, in a typical bone, relative to the outer lip, six millimetres deeper below, five millimetres deeper in front, and practically equal to it in the upper part. The angle, then, is clearly caused by the shape of the inner lip, and it will be found that by cutting away the outer lip, still leaving the inner lip, the carrying angle and its disappearance remain as they were before the removal of this part of bone. The reason of the existence of the carrying angle is, probably, this. Not only does its presence enable the extended upper limb to swing clear of the body, but it allows the clear swing to take place even when the hand is fully pronated, and more so when it is only semi-pronated. The angle might be thought to disappear when the hand is pronated, but the disappearance is imaginary, and is due to the radius coming across the ulna, and thus masking the angle. This statement raises the point which it is desired to make in this paper. The existence of the carrying angle enables the pronated hand to be kept in the same axis as that of the upper arm, and, thus, to add very much to the strength of a thrust with the upper limb, and, conversely, to a pull. In this way, only, is it to be explained, and not by reference to the carrying of weights, except in so far as the hand is pronated in so doing. The presence of a carrying angle is recognised by surgeons, who refer to it by the term "cubitus valgus." This is, surely, a bad expression as with the analogous terms of "hallux" and "pes valgus" it will indicate to the student that there is something pathological about the carrying angle, which there certainly is not.

The study of the angle, in the monkeys, is very interesting. I plead guilty to a prejudice against these "poor relations," but I think it will be admitted that the upper limb of monkeys is not as fine a product as that of man. The monkeys appear to have a good carrying angle, but the appearance, like some of their actions, is deceptive. The monkeys possess a carrying angle, but we must not be led astray by the appearance of an angle until we have examined their humerus.

Through the kindness of Dr Sontagde, of the Zoological Gardens, London, and of Prof. J. P. Hill (whose continued kindness to me I should like to acknowledge) I have been enabled to examine three different kinds of monkey, viz.: *Macacus rhesus*, *Cercocebus fuliginosus*, and baboon, and it is quite clear

that in these three animals the direction of the head of the humerus is different to that of the head in man's humerus.

The articular surface of the head of the humerus of a monkey points in the same direction as the olecranon fossa, almost directly backwards; whereas that of man is directed inwards and backwards, and does not point in the same direction as the olecranon fossa. Relative, then, to man, the upper limb of the monkeys must be rotated outwards. Slight flexion of the elbow will then give an impression of a very large carrying angle in the monkey, when, in fact, it is not as large as that of man.

The carrying angle is present at all ages in man, and is found in full term foetuses, and in quite young children, and this observation is particularly interesting, as the strength of the upper limb is of prime importance to the young child. It is, therefore, with much regret, that in Prof. Wood Jones' charming work on *Arboreal Man*, I find an illustration of a new-born baby (fig. 76), and of a child aged eighteen months (fig. 77) in both of which there is no carrying angle apparent.

(2) *The division of the joint into two parts.* This is suggested by the transverse groove or line, which runs across the greater sigmoid cavity of the ulna, but there is almost an equally obvious suggestion of such a division in the lower end of the humerus. The outer lip of the trochlea is not a continuous ridge, for it is broken at the junction of its posterior two-fifths, and the anterior three-fifths. At this point there is very often a prominent tubercle. I do not doubt but that this tubercle is perfectly well known, but I am sure that I did not realise its exact significance until I had examined the joint by an indirect method and in the following manner. A thick flat mass of plasticine is laid on the table, and the lower end of the humerus, in the position of extension, is laid upon it. It is pressed firmly down, and the humerus is then carefully rotated in a wheel-like manner on the plasticine. It is moved through 180 degrees. At the end of the movement the bone is in the position which it would occupy in the position of flexion of the joint. Great care must be taken that the bone in being rotated, does not slip forwards. The slipping forwards may be prevented by putting several pins at regular intervals in the circumference of the inner lip of the trochlea, or, better still, by driving tin plates into it. If firm pressure be made whilst the rotation is thus being carried out, a very good picture of the joint surface is obtained on the surface of the plasticine. The size of the impression will vary as the actual size of the circumference upon which the movement is made, but with this reservation we need not further consider the size of the impression. When we study such an impression, one important fact is at once apparent.

This fact is quite obvious on the bone but is brought out really better on the impression. The capitellum cuts into the trochlea in a most pronounced way, and the tubercle which has been mentioned is situated behind the capitellum, and does not lie on its inner side as might have been expected. The mere fact that the capitellum does not extend back as far as the trochlea



must be taken as an indication that the humerus as well as the ulna shows a division of the joint into two parts, a division which is indicated on the ulna by the transverse groove which runs across its greater sigmoid cavity. But the division of the joint into two parts is also indicated by the tubercle which has just been mentioned, for at the point where this tubercle is developed the external lip of the trochlea is interrupted. If the ridge which terminates in the tubercle were prolonged directly forwards, it might, in some cases, cut off as much as the inner third of the capitellum. By this amount, therefore, the capitellum will cut into the trochlea. No attempt is made to deny that the olecranon portion of the greater sigmoid cavity may not take part in the movements of the joint, but, it may be stated that this part of the joint is chiefly concerned with the security of the joint during its movement, and especially during the completion of extension. It is well known that writers have stated, and denied, that there is a screw movement in the joint, but this must not be taken to mean that there is a wobbling of the joint when it is moved. As extension is being brought about the upper part of the cavity clutches, with a lateral pressure, the back part of the trochlea in such a way that the pressure is transmitted inwards, and my reason for making this statement is as follows. If the radius be removed from the articulation, it will readily be observed that there is a considerable portion of the outer part of the greater sigmoid cavity which is exposed in flexion, and that when extension is made and completed, this surface which is at a considerable angle with the rest of the upper part of the articular surface, is covered by the outer lip of the trochlea, and, in fact, by that part of the trochlea which terminates in the tubercle. As this is happening a considerable pressure will be obviously directed inwards, and we are now in a position to explain the third point which is raised in the argument of this paper. But before this little question is answered an additional feature in the joint surface is to be noted. There is an accessory articular surface of the greater sigmoid cavity situated on the outer part of that portion of the cavity, and lying below the transverse groove which runs across the cavity. This accessory part lies above the lesser sigmoid cavity, and the tubercle, which has been noticed, lies against it in extreme extension of the joint. It is triangular in outline with its base directed inwards, and, as flexion takes place, it becomes entirely uncovered.

(3) *The presence of an apophysis on the inner side of the trochlea of the humerus.* It is, of course, well known that an apophysis extends downwards from the shaft of the humerus between the trochlea and the internal condyle of the bone. That the apophysis is developed in connection with the inward pressure, which we have seen is exerted in an inward direction, would appear to be an obvious point and requires no further labouring.

(4) *The limitation of flexion of the joint.* Some authorities think that limitation of flexion is brought about by the soft structures on the front of the joint coming into contact with one another. Although I am perfectly willing to accept the statement as true, I should have thought that whilst

muscle sense would have informed us when we had moved the joint sufficiently in the direction of flexion, pressure on the muscles, and also on the artery and vein and nerves is hardly the way in which extreme flexion is controlled. Now, if the lower extremity of the humerus be examined, it will be found that there is a well marked ridge between the coronoid fossa, and the small fossa above the capitellum. In the recent state this ridge is covered with cartilage, and the outer part of the coronoid comes into collision with it when the joint is fully flexed. This limitation is brought about before the soft parts are pressed upon to any great extent. It is not without significance that the particular part of the coronoid concerned in taking the pressure is supported by a ridge which is perfectly well known as the tuberosity of the ulna.

### *The radio-ulna joints*

(5) *There is a deepening of the circumferential articular surface on the inner side of the head of the radius.* What the exact significance of this may be I am not prepared to say, but, as a matter of fact, when the forearm is fully supinated, the tendon of the biceps lies against it, and may be stretched over it, and thus may be responsible for the extension of the surface in this region, in the same way as the tendon of the ilio-psoas may be responsible for the prolongation of the articular surface of the head of the femur on its front aspect. (I am aware that there are many distinguished anatomists who do not share this view, but I have seen a case in which there was considerable softening of the hip-joint as a result of disease, and the tendon of the ilio-psoas had cut into the femur in the region where the extension of the articular surface on the front of the neck normally takes place.)

(6) *The sacciform nature of the synovial cavities of the upper and lower radio-ulnar joints.* The probable explanation of this peculiarity is as follows. If when viewed from the side the outline of the capitellum suggested a perfect sphere there might be no need for the loose cavities which are present in these joints; but the outline is far from being circular, and, thus, there must be some upward and downward movement of the radius upon the ulna in the movements of the elbow-joint, and it is to this upward and downward movement that the sacciform nature of these joints is due.

The observations in this paper may be summarised as follows:

(1) The formation of the carrying angle is due to the varying depth of the internal lip of the trochlea, when compared with the depth of the external lip. During flexion of the elbow this angle is not converted into an eating angle. The reason for the presence of the carrying angle is to be found in the better mechanical condition which exists during pronation of the hand.

(2) The joint is divided into two parts as is indicated by the transverse groove which runs across the greater sigmoid cavity of the ulna, and also, on the humerus by the posterior margin of the capitellum, and by the tubercle on the lower end of the bone.

(3) The formation of the apophysis at the lower end of the humerus is to be referred to the greater pressure which is exercised upon the inner lip of the trochlea, when compared with that upon the outer lip.

(4) Extreme flexion is limited, in movements of the elbow joint by the meeting of the humerus and ulna.

(5) The increased vertical extent of the inner portion of the circumferential articular surface of the head of the radius may be due to its contact with the biceps muscle in supination of the forearm.

(6) The sacciform nature of the synovial cavities of the upper and lower radio-ulnar joints is due to the upward and downward movement of the radius upon the ulna in flexion and extension of the elbow-joint.

My only excuse for writing this paper which is based upon a demonstration of the movements of the elbow-joint which I was enabled to give before the Anatomical Society at Cambridge, is the possession of several fresh joints, and their study through several years.



# LENGTH OF LONG BONES AND THEIR PROPORTION TO BODY HEIGHT IN HINDUS

BY PROFESSOR N. PAN,  
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As there are no records of the length of long bones in Indians and their proportion to body height, I intend to publish my observations on this subject. A series of measurements has been taken on 142 subjects, including males and females. These subjects were brought to the dissecting hall of the Medical College, Calcutta, and all of them were adult Hindus, chiefly of Bengal, Behar and Orissa.

## *Body length*

The length of the body has been measured, with the scalp and soft parts of the soles of the feet intact. In Table "A," the subjects have been arranged in order of their stature. It will be observed that there are altogether 142 subjects, of which 86 are males and 56 females. The body length ranges from 70" to 55", giving an average of 62", taking the males and females together. The average stature of an Englishman, according to Galton (*Life Hist. Album*), is 68". According to Dr Humphry (*The Human Skeleton*), the average height of an adult European is 65", so the average stature of a Hindu is shorter by 3" to 6". The table shows at a glance that the body height is much greater in males, as the subjects towards the beginning of the table are mostly males, whereas the subjects towards the end of the table are mostly females. Taking the average height of the males and females separately, it is found that in the former it is roughly 64" (63·8"), and in the latter 59".

## *Length of the long bones*

The length of the femur, tibia, fibula, humerus, radius and ulna has been measured in the fresh state with the articular ends covered with cartilages.

## *Femur*

The length represents the distance between the articular surfaces at the two ends. The length varies from 14" to 18½", giving an average of 16·2", taking the males and females together. Taking the two sexes separately, the average length in males is 16·7" and in females 15·5". The proportion to body length varies from 29·3 to 23 per cent., giving an average of 26·2 per cent.—whether the sexes are taken together or separately.

*Tibia*

The length represents the distance between the articular surface of the head and tip of the medial malleolus. The length varies from 12" to 16", giving an average of 13·8" when both sexes are taken together. In males, the average length is 14·2" and in females 13·2". The proportion to body length varies from 25 to 19·4 per cent., giving an average of 22·3 per cent. when both males and females are taken together. Taking the two sexes separately, there is no difference in the proportion to body height, the average being the same in both sets of cases as in the femur.

*Fibula*

The length has been calculated from the tip of the styloid process to the tip of the lateral malleolus. The length varies from 12" to 16½", giving an average of 13·9" when both males and females are taken together. In males, the average length is 14·3", while in females it is 13·3". The proportion to body length varies from 25·4 to 20 per cent., giving an average of 22·4 per cent. when both males and females are taken together or separately.

*Humerus*

The length has been measured between the articular surfaces. It varies from 9½" to 13½", giving an average of 11·6", when both sexes are taken together. In males, the average length is 12", whereas in females it is 11·1". The proportion to body length varies from 15·9 to 20·7 per cent., giving an average of 18·8 per cent., when both sexes are taken together or separately.

*Radius*

The length has been measured between the articular surface at the top of the head and the tip of the styloid process. It varies from 8" to 10½", giving an average of 9", taking males and females together. In males, the average length is 9·5", whereas in females it is 8·8". The proportion to body length varies from 12·9 to 17·3 per cent., giving an average of 15·1 per cent. when both sexes are taken together or separately.

*Ulna*

The length has been measured from superior surface of the olecranon to the tip of the styloid process at the lower end. It varies from 8½" to 11½", giving an average of 10·2" when males and females are taken together. In males the average length is 10·5", while in females it is 9·7". The proportion to body length varies from 14·4 to 19 per cent., giving an average of 16·4 per cent., whether the two sexes are taken together or separately.

Table A

The subjects have been arranged in order of their body length.

The measurements are in inches.

L. = length, P. = proportion to body length calculated to a scale of 100.

No.	Sex	Body L.	Femur L.—P.	Tibia L.—P.	Fibula L.—P.	Humerus L.—P.	Radius L.—P.	Ulna L.—P.
1	M.	70	18 —25.7	16 —22.9	15 $\frac{1}{2}$ —22.1	13 $\frac{1}{2}$ —19.3	10 $\frac{1}{2}$ —15	11 $\frac{1}{2}$ —16.8
2	M.	69	18 $\frac{1}{2}$ —26.8	15 $\frac{1}{2}$ —22.5	15 —21.7	12 $\frac{1}{2}$ —18.1	10 $\frac{1}{2}$ —14.9	11 $\frac{1}{2}$ —16.7
3	M.	69	16 $\frac{1}{2}$ —23.9	15 $\frac{1}{2}$ —22.1	15 —21.7	12 —17.4	9 $\frac{3}{4}$ —14.1	10 $\frac{1}{2}$ —15.2
4	M.	69	17 $\frac{1}{2}$ —25.4	15 —21.7	15 $\frac{1}{2}$ —22.5	12 —17.4	10 $\frac{1}{2}$ —15.2	11 $\frac{1}{2}$ —16.7
5	M.	68	17 —25	16 —23.5	16 $\frac{1}{2}$ —24.2	12 $\frac{1}{2}$ —18.4	10 $\frac{1}{2}$ —15.4	11 $\frac{1}{2}$ —16.5
6	M.	68	16 $\frac{1}{2}$ —24.3	13 $\frac{1}{2}$ —19.9	13 $\frac{3}{4}$ —20.2	13 —19.1	10 $\frac{1}{2}$ —15.4	11 $\frac{1}{2}$ —16.9
7	M.	68	18 —26.5	14 —20.6	14 —20.6	12 $\frac{1}{2}$ —18.4	9 $\frac{3}{4}$ —14.3	10 $\frac{1}{2}$ —15.8
8	M.	68	17 $\frac{1}{2}$ —25.7	14 —20.6	14 —20.6	13 $\frac{1}{2}$ —19.9	9 $\frac{3}{4}$ —14	10 $\frac{1}{2}$ —15.4
9	M.	68	17 $\frac{1}{2}$ —25.7	15 —22.1	15 $\frac{1}{2}$ —22.8	12 $\frac{1}{2}$ —18.4	10 —14.7	11 $\frac{1}{2}$ —16.5
10	M.	68	18 —26.5	14 $\frac{1}{2}$ —21.3	14 $\frac{1}{2}$ —21.3	13 —19.1	10 $\frac{1}{2}$ —15.4	11 —16.2
11	M.	67	17 —25.4	15 $\frac{1}{2}$ —22.8	15 —22.4	11 —16.4	9 —13.4	9 $\frac{3}{4}$ —14.6
12	M.	67	17 $\frac{1}{2}$ —26.1	15 $\frac{1}{2}$ —23.1	15 —22.4	13 —19.4	10 $\frac{1}{2}$ —15.7	11 $\frac{1}{2}$ —17.2
13	M.	67	17 $\frac{1}{2}$ —26.1	15 —22.4	15 $\frac{1}{2}$ —23.1	12 —17.9	10 $\frac{1}{2}$ —15.7	11 —16.4
14	M.	67	16 —23.9	14 $\frac{1}{2}$ —21.6	15 —22.4	11 $\frac{1}{2}$ —17.2	10 —14.9	11 —16.4
15	M.	67	16 $\frac{1}{2}$ —25	15 —22.4	15 $\frac{1}{2}$ —22.8	13 —19.4	10 $\frac{1}{2}$ —15.7	11 $\frac{1}{2}$ —16.8
16	M.	66 $\frac{1}{2}$	17 $\frac{1}{2}$ —26.7	15 —22.5	14 $\frac{1}{2}$ —21.8	13 —19.5	10 $\frac{1}{2}$ —15.4	11 —16.5
17	M.	66	16 $\frac{1}{2}$ —25	13 $\frac{3}{4}$ —20.8	13 $\frac{1}{4}$ —20.1	12 —18.1	9 $\frac{3}{4}$ —14.8	10 $\frac{1}{2}$ —15.5
18	F.	66	18 —27.3	16 —24.2	16 —24.2	13 $\frac{1}{4}$ —20.1	10 —15.1	10 $\frac{1}{2}$ —16.3
19	M.	66	17 —25.8	15 —22.7	15 —22.7	12 $\frac{1}{2}$ —18.9	10 $\frac{1}{2}$ —15.5	11 $\frac{1}{2}$ —17.4
20	F.	66	18 —27.3	15 —22.7	15 —22.7	12 $\frac{1}{2}$ —18.9	10 $\frac{1}{2}$ —15.9	11 —16.7
21	M.	66	18 —27.3	16 —24.2	15 $\frac{1}{2}$ —23.9	12 $\frac{1}{2}$ —18.9	10 $\frac{1}{2}$ —15.9	11 —16.7
22	M.	66	17 —25.8	15 —22.7	15 —22.7	12 —18.2	10 —15.1	11 —16.7
23	M.	66	17 —25.8	15 —22.7	15 —22.7	13 —19.7	9 $\frac{3}{4}$ —14.8	11 —16.7
24	M.	66	17 $\frac{1}{2}$ —26.5	14 —21.2	14 $\frac{1}{4}$ —21.6	10 $\frac{1}{2}$ —15.9	8 $\frac{3}{4}$ —12.9	9 $\frac{1}{2}$ —14.4
25	M.	66	18 —27.3	14 $\frac{1}{2}$ —21.6	14 $\frac{1}{2}$ —22.4	12 —18.1	10 —15.1	10 $\frac{1}{2}$ —15.9
26	M.	65	16 $\frac{3}{4}$ —25.8	13 $\frac{1}{2}$ —20.8	13 $\frac{1}{2}$ —20.8	13 —20	9 $\frac{1}{2}$ —14.6	10 $\frac{1}{2}$ —16.2
27	M.	65	15 —23.1	13 $\frac{1}{2}$ —20.4	13 —20	12 $\frac{1}{4}$ —18.8	9 $\frac{1}{2}$ —14.6	10 $\frac{1}{2}$ —16.2
28	M.	65	17 $\frac{1}{2}$ —26.9	15 —23.1	15 —23.1	12 —18.5	10 —15.4	10 $\frac{1}{2}$ —16.2
29	M.	65	17 —26.2	14 $\frac{1}{2}$ —22.3	14 $\frac{1}{2}$ —22.3	12 $\frac{1}{2}$ —19.2	10 $\frac{1}{2}$ —16.2	11 $\frac{1}{2}$ —17.7
30	M.	65	16 $\frac{1}{2}$ —25.4	14 $\frac{1}{2}$ —21.9	14 $\frac{1}{2}$ —22.7	12 $\frac{1}{2}$ —18.8	9 $\frac{1}{2}$ —14.6	10 $\frac{1}{2}$ —15.8
31	M.	65	16 $\frac{1}{2}$ —25.4	14 —21.5	14 —21.5	12 $\frac{1}{2}$ —19.2	10 —15.4	11 —16.9
32	M.	65	16 —24.6	14 —21.5	14 $\frac{1}{2}$ —22.3	12 $\frac{1}{4}$ —18.8	9 $\frac{1}{2}$ —14.6	10 $\frac{1}{2}$ —16.5
33	M.	65	16 —24.6	13 $\frac{1}{2}$ —20.8	14 —21.5	12 —18.5	9 $\frac{1}{2}$ —15	10 $\frac{1}{2}$ —15.8
34	M.	65	16 —24.6	14 —21.5	14 $\frac{1}{2}$ —22.3	12 —18.5	10 —15.4	10 $\frac{1}{2}$ —16.5
35	M.	65	16 $\frac{1}{2}$ —25.4	14 —21.5	14 —21.5	12 —18.5	10 —15.4	11 —16.9
36	M.	65	16 —24.6	14 $\frac{1}{2}$ —22.3	15 $\frac{1}{4}$ —23.5	12 $\frac{1}{2}$ —19.2	10 —15.4	11 —16.9
37	M.	65	17 —26.2	14 —21.5	14 $\frac{1}{2}$ —22.1	12 —18.5	9 $\frac{1}{2}$ —14.6	10 $\frac{1}{2}$ —15.8
38	M.	64 $\frac{1}{2}$	17 —26.4	15 $\frac{1}{2}$ —24	15 $\frac{1}{2}$ —24	11 —17	9 $\frac{1}{2}$ —14.7	10 —15.3
39	M.	64 $\frac{1}{2}$	16 $\frac{1}{2}$ —25.8	14 $\frac{1}{2}$ —22.5	14 $\frac{1}{2}$ —22.5	12 $\frac{1}{2}$ —19.4	9 $\frac{1}{2}$ —15.1	10 $\frac{1}{2}$ —16.3
40	M.	64	17 —26.7	15 —23.4	15 —23.4	12 —18.7	10 $\frac{1}{2}$ —16.4	11 —17.2
41	M.	64	17 —26.7	13 $\frac{3}{4}$ —21.5	14 —21.9	12 $\frac{1}{2}$ —19.5	10 —15.6	11 —17.2
42	M.	64	16 $\frac{3}{4}$ —26.2	15 —23.4	14 $\frac{1}{2}$ —23	12 $\frac{1}{2}$ —19.9	10 —15.6	11 $\frac{1}{2}$ —18
43	M.	64	17 —26.7	14 —21.9	13 $\frac{3}{4}$ —21.5	10 $\frac{1}{2}$ —16	8 $\frac{3}{4}$ —13.7	9 $\frac{1}{2}$ —15.2
44	M.	64	16 $\frac{1}{2}$ —25.4	14 $\frac{1}{2}$ —22.7	14 $\frac{1}{2}$ —22.7	12 —18.7	9 $\frac{1}{2}$ —15.2	10 $\frac{1}{2}$ —16.4
45	M.	64	16 $\frac{1}{2}$ —25.8	14 —21.9	14 —21.9	11 $\frac{1}{2}$ —18	9 —13.8	10 —15.6
46	M.	64	17 —26.7	14 —21.9	14 —21.9	12 $\frac{1}{2}$ —19.5	10 —15.6	11 —17.2
47	M.	64	16 $\frac{1}{2}$ —26.2	14 $\frac{1}{2}$ —22.7	14 $\frac{1}{2}$ —23	12 $\frac{1}{2}$ —19.9	10 $\frac{1}{2}$ —16.4	11 $\frac{1}{2}$ —18
48	M.	64	17 $\frac{1}{2}$ —27	15 $\frac{1}{2}$ —23.8	15 $\frac{1}{2}$ —23.8	12 —18.7	9 $\frac{1}{2}$ —14.8	10 $\frac{1}{2}$ —16
49	M.	64	18 $\frac{1}{2}$ —28.9	15 $\frac{1}{2}$ —24.2	15 $\frac{1}{2}$ —24.2	12 $\frac{1}{2}$ —19.5	10 $\frac{1}{2}$ —16.4	11 $\frac{1}{2}$ —18
50	M.	64	17 $\frac{1}{2}$ —27.3	14 $\frac{1}{2}$ —22.7	15 —23.4	12 $\frac{1}{2}$ —19.5	9 $\frac{1}{2}$ —14.8	11 —17.2
51	M.	64	16 —25	14 $\frac{1}{2}$ —22.7	15 —23.4	11 $\frac{1}{2}$ —18	10 —15.6	11 —17.2
52	M.	64	15 $\frac{1}{2}$ —24.6	13 $\frac{1}{2}$ —21.5	13 $\frac{1}{2}$ —21.1	12 —18.7	9 $\frac{1}{2}$ —14.8	10 $\frac{1}{2}$ —16.4
53	M.	63	17 $\frac{1}{2}$ —27.4	14 $\frac{1}{2}$ —22.6	14 —22.2	12 $\frac{1}{2}$ —19.8	9 $\frac{1}{2}$ —15.5	11 —17.5
54	F.	63	16 —25.4	14 $\frac{1}{2}$ —23	14 $\frac{1}{2}$ —23	11 $\frac{3}{4}$ —18.7	9 $\frac{1}{2}$ —15.1	10 —16
55	M.	63	17 $\frac{1}{2}$ —27.4	14 —22.2	14 —22.2	12 —19	10 —16	11 —17.5
56	M.	63	17 $\frac{1}{2}$ —27.8	15 —23.8	14 $\frac{1}{2}$ —23.4	12 $\frac{1}{2}$ —19.8	9 $\frac{1}{2}$ —15.5	11 —17.5
57	F.	63	15 —23.8	13 —20.6	13 $\frac{1}{2}$ —21	10 $\frac{1}{2}$ —16.6	8 $\frac{1}{2}$ —13.5	9 $\frac{1}{2}$ —14.7
58	M.	63	16 —25.4	14 —22.2	13 $\frac{1}{2}$ —21.4	12 —19	9 $\frac{1}{2}$ —14.7	10 $\frac{1}{2}$ —16.3
59	F.	63	17 $\frac{1}{2}$ —27.8	15 —23.8	15 —23.8	11 —17.5	9 —14.3	10 —15.9



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No.	Sex	Body L.	Femur L.—P.	Tibia L.—P.	Fibula L.—P.	Humerus L.—P.	Radius L.—P.	Ulna L.—P.
60	M.	63	14 $\frac{1}{2}$ —23	13 —20·6	13 —20·6	11 —17·5	8 $\frac{1}{2}$ —13·5	9 $\frac{1}{2}$ —15·1
61	M.	63	16 $\frac{1}{2}$ —26·2	14 —22·2	13 $\frac{1}{2}$ —21·4	11 $\frac{1}{2}$ —18·3	9 $\frac{1}{2}$ —14·7	10 —15·9
62	M.	63	15 $\frac{1}{2}$ —24·6	14 —22·2	14 —22·2	11 $\frac{1}{2}$ —18·3	9 $\frac{1}{2}$ —15·1	10 $\frac{1}{2}$ —16·6
63	M.	62 $\frac{1}{2}$	18 $\frac{1}{2}$ —29·2	15 —24	14 $\frac{3}{4}$ —23·6	12 —19·2	10 —16	11 —17·6
64	M.	62	15 $\frac{1}{2}$ —25·4	13 $\frac{1}{2}$ —21·4	13 —21	11 $\frac{1}{2}$ —18·5	9 $\frac{1}{2}$ —15·3	10 —16·1
65	M.	62	16 —25·8	13 $\frac{1}{2}$ —21·8	13 $\frac{1}{2}$ —21·4	11 —17·7	8 $\frac{1}{2}$ —13·7	9 $\frac{1}{2}$ —15·3
66	M.	62	17 $\frac{1}{2}$ —28·2	13 $\frac{1}{2}$ —21·8	13 $\frac{1}{2}$ —22·2	12 —19·4	9 $\frac{1}{2}$ —15·3	10 —16·1
67	M.	62	16 —25·8	14 —22·6	14 —22·6	12 —19·4	9 —14·5	10 —16·1
68	F.	62	17 —27·4	14 —22·6	14 —22·6	11 $\frac{1}{2}$ —18·5	9 $\frac{1}{2}$ —15·3	10 $\frac{1}{2}$ —16·9
69	F.	62	16 $\frac{1}{2}$ —26·6	14 —22·6	14 —22·6	11 $\frac{1}{2}$ —18·5	8 —12·9	9 $\frac{1}{2}$ —15·3
70	M.	62	16 $\frac{1}{2}$ —26·6	13 —21	13 —21	11 $\frac{1}{2}$ —18·5	9 —14·5	10 —16·1
71	M.	62	16 $\frac{1}{2}$ —26·6	14 —22·6	13 $\frac{1}{2}$ —21·8	12 —19·4	9 $\frac{1}{2}$ —15·3	10 —16·1
72	M.	62	16 —25·8	14 —22·6	14 —22·6	11 —17·7	9 $\frac{1}{2}$ —15·3	10 —16·1
73	M.	62	16 $\frac{1}{2}$ —26·2	15 —24·2	14 $\frac{3}{4}$ —23·4	12 —19·4	9 $\frac{1}{2}$ —15·3	10 $\frac{1}{2}$ —16·9
74	F.	62	16 —25·8	14 $\frac{1}{2}$ —23·4	14 —22·6	11 —17·7	9 —14·5	10 —16·1
75	F.	62	15 —24·2	12 —19·4	12 $\frac{1}{2}$ —20·2	12 —19·4	10 —16·1	10 —17·7
76	M.	62	16 $\frac{1}{2}$ —26·6	14 —22·6	14 $\frac{1}{2}$ —23	12 —19·4	9 $\frac{1}{2}$ —15·3	10 $\frac{1}{2}$ —16·9
77	M.	62	16 $\frac{1}{2}$ —26·6	14 —22·6	14 $\frac{1}{2}$ —23	11 $\frac{1}{2}$ —18·5	8 $\frac{1}{2}$ —13·7	10 —16·1
78	M.	61 $\frac{1}{2}$	17 —27·6	14 —22·8	14 —22·8	11 —17·9	9 —14·6	10 —16·3
79	F.	61 $\frac{1}{2}$	16 $\frac{1}{2}$ —26·8	13 $\frac{3}{4}$ —22·4	13 $\frac{1}{2}$ —22	11 $\frac{1}{2}$ —18·7	8 $\frac{1}{2}$ —13·8	10 $\frac{1}{2}$ —17·1
80	M.	61 $\frac{1}{2}$	16 $\frac{1}{2}$ —26·8	14 —22·8	13 $\frac{1}{2}$ —22	11 —17·9	9 —14·6	10 $\frac{1}{2}$ —16·6
81	F.	61	15 —24·6	12 $\frac{1}{2}$ —20·5	12 $\frac{1}{2}$ —20·5	10 $\frac{1}{2}$ —17·2	8 —13·1	9 —14·7
82	M.	61	16 —26·2	14 —23	14 —23	11 $\frac{1}{2}$ —18·8	9 $\frac{1}{2}$ —15·6	9 $\frac{1}{2}$ —16
83	M.	61	16 $\frac{1}{2}$ —27	13 $\frac{1}{2}$ —21·7	14 —23	11 $\frac{1}{2}$ —19·3	9 $\frac{1}{2}$ —15·2	10 $\frac{1}{2}$ —17·2
84	M.	61	16 $\frac{1}{2}$ —27·5	15 —24·6	14 $\frac{3}{4}$ —24·2	12 $\frac{1}{2}$ —20·1	10 —16·4	11 —18
85	M.	61	16 $\frac{1}{2}$ —27	13 $\frac{1}{2}$ —22·1	13 $\frac{1}{2}$ —21·7	11 $\frac{1}{2}$ —18·4	9 $\frac{1}{2}$ —15·2	10 —16·4
86	M.	61	16 —26·2	14 —23	14 $\frac{1}{2}$ —23·8	12 —19·7	10 $\frac{1}{2}$ —17·2	11 —18
87	F.	61	16 —26·2	13 $\frac{1}{2}$ —22·1	13 $\frac{1}{2}$ —22·1	12 —19·7	9 $\frac{1}{2}$ —15·2	10 $\frac{1}{2}$ —17·2
88	M.	61	16 —26·2	15 —24·6	15 $\frac{1}{2}$ —25	12 —19·7	9 $\frac{1}{2}$ —15·6	10 $\frac{1}{2}$ —16·8
89	M.	60 $\frac{1}{2}$	16 $\frac{1}{2}$ —27·3	13 $\frac{1}{2}$ —22·3	13 $\frac{1}{2}$ —22·7	12 —19·8	9 $\frac{1}{2}$ —15·7	10 $\frac{1}{2}$ —17·4
90	F.	60	17 $\frac{1}{2}$ —29·2	14 $\frac{1}{2}$ —24·2	14 $\frac{1}{2}$ —24·2	11 —18·3	8 $\frac{1}{2}$ —14·2	9 $\frac{1}{2}$ —15·8
91	F.	60	15 $\frac{1}{2}$ —25·4	13 $\frac{1}{2}$ —22·1	13 —21·7	11 —18·3	8 $\frac{1}{2}$ —14·2	9 $\frac{1}{2}$ —15·8
92	M.	60	15 $\frac{1}{2}$ —25·8	13 $\frac{1}{2}$ —22·9	13 $\frac{1}{2}$ —22·9	11 $\frac{1}{2}$ —19·6	9 —15	10 —16·6
93	M.	60	16 —26·6	14 —23·3	13 $\frac{1}{2}$ —22·9	11 $\frac{1}{2}$ —19·1	8 $\frac{3}{4}$ —14·6	9 $\frac{1}{2}$ —15·8
94	F.	60	15 —25	14 —23·3	14 —23·3	11 —18·3	9 $\frac{1}{2}$ —15·4	10 —16·6
95	F.	60	16 —26·6	13 —21·6	13 —21·6	11 $\frac{1}{2}$ —19·2	9 —15	10 —16·6
96	F.	60	16 $\frac{1}{2}$ —27·5	13 —21·6	13 $\frac{1}{2}$ —22·5	11 $\frac{1}{2}$ —18·7	9 —15	10 —16·6
97	F.	60	15 —25	13 —21·6	13 —21·6	10 $\frac{1}{2}$ —17·1	8 $\frac{1}{2}$ —14·2	9 —15
98	M.	60	16 —26·7	13 —21·6	13 $\frac{1}{2}$ —22·1	11 $\frac{1}{2}$ —19·2	8 $\frac{1}{2}$ —14·6	10 —16·6
99	F.	60	15 $\frac{1}{2}$ —25·8	12 $\frac{1}{2}$ —20·8	13 —21·6	10 —16·6	8 —13·3	9 $\frac{1}{2}$ —15·5
100	F.	60	16 $\frac{1}{2}$ —27·5	14 —23·3	14 —23·3	11 —18·3	8 —13·3	9 $\frac{1}{2}$ —15·8
101	F.	60	15 —25	13 $\frac{1}{2}$ —22·1	13 —21·6	10 $\frac{3}{4}$ —17·9	8 $\frac{1}{2}$ —14·2	9 $\frac{1}{2}$ —15·4
102	F.	60	15 —25	13 —21·6	13 —21·6	11 $\frac{1}{2}$ —19·2	9 —15	9 $\frac{1}{2}$ —16·2
103	M.	60	16 —26·7	14 —23·3	14 —23·3	12 —20	9 $\frac{1}{2}$ —16·2	10 $\frac{1}{2}$ —17·5
104	M.	60	15 $\frac{1}{2}$ —25·8	13 $\frac{1}{2}$ —22·5	13 —21·6	11 —18·3	9 —15	10 —16·6
105	F.	59	15 —25·4	13 —22	12 $\frac{1}{2}$ —21·1	10 $\frac{1}{2}$ —17·8	8 $\frac{1}{2}$ —14·4	9 —15·2
106	F.	59	15 $\frac{1}{2}$ —25·8	13 $\frac{1}{2}$ —22·9	13 —22	10 $\frac{1}{2}$ —17·8	8 $\frac{1}{2}$ —14	9 —15·2
107	F.	59	15 —25·4	13 —22	13 —22	11 —18·6	8 $\frac{1}{2}$ —14·4	9 $\frac{1}{2}$ —16·1
108	M.	59	16 —27·1	13 —22	13 $\frac{1}{2}$ —22·5	12 —20·3	9 $\frac{1}{2}$ —16·1	10 —16·9
109	F.	59	15 —25·4	13 $\frac{1}{2}$ —22·9	13 $\frac{1}{2}$ —22·9	11 $\frac{1}{2}$ —19·5	9 —15·3	10 —16·9
110	F.	59	15 $\frac{1}{2}$ —26·3	14 —23·7	14 $\frac{1}{2}$ —24·2	10 —16·9	8 —13·6	8 $\frac{3}{4}$ —14·8
111	F.	58 $\frac{1}{2}$	15 $\frac{1}{2}$ —26·9	13 —22·2	12 $\frac{3}{4}$ —21·8	12 —20·5	10 —17·1	11 —18·8
112	F.	58 $\frac{1}{2}$	15 —25·6	12 $\frac{3}{4}$ —21·8	12 $\frac{3}{4}$ —21·8	10 $\frac{1}{2}$ —17·9	8 $\frac{1}{2}$ —14·1	9 —15·4
113	F.	58 $\frac{1}{2}$	15 $\frac{1}{2}$ —26·5	13 $\frac{1}{2}$ —22·6	13 $\frac{1}{2}$ —23·5	11 $\frac{1}{2}$ —19·7	8 $\frac{1}{2}$ —14·5	9 $\frac{1}{2}$ —15·8
114	F.	58	13 $\frac{3}{4}$ —23·3	12 $\frac{1}{2}$ —21·5	12 $\frac{1}{2}$ —21·1	10 $\frac{1}{2}$ —18·1	8 $\frac{1}{2}$ —14·6	9 —15·5
115	F.	58	17 —29·3	14 —24·1	14 —24·1	12 —20·7	9 —15·5	10 —17·2
116	F.	58	15 —25·9	13 $\frac{1}{2}$ —23·2	13 —22·4	11 —19	9 —15·5	10 —17·2
117	F.	58	15 $\frac{1}{2}$ —26·3	13 —22·4	13 $\frac{1}{2}$ —22·8	11 —19	8 $\frac{1}{2}$ —14·6	9 $\frac{1}{2}$ —16·8
118	F.	58	16 —27·6	13 $\frac{1}{2}$ —23·2	14 —24·1	11 $\frac{1}{2}$ —19·4	9 —15·5	9 $\frac{1}{2}$ —16·8
119	F.	58	16 —27·6	14 $\frac{1}{2}$ —25	14 $\frac{1}{2}$ —25·4	11 $\frac{1}{2}$ —19·8	9 $\frac{1}{2}$ —16·4	10 $\frac{1}{2}$ —17·7
120	F.	58	16 $\frac{1}{2}$ —28·4	14 —24·1	14 $\frac{1}{2}$ —25	12 —20·7	10 —17·2	11 —19
121	F.	58	15 —25·9	13 $\frac{1}{2}$ —23·3	13 $\frac{1}{2}$ —23·3	12 —20·7	9 $\frac{1}{2}$ —16·4	10 $\frac{1}{2}$ —18·1
122	F.	58	15 $\frac{1}{2}$ —26·3	13 —22·4	13 $\frac{1}{2}$ —22·8	11 $\frac{1}{2}$ —19·8	8 $\frac{3}{4}$ —15·1	9 $\frac{1}{2}$ —16·4
123	F.	57 $\frac{1}{2}$	15 —26·1	13 —22·6	12 $\frac{3}{4}$ —22·2	10 $\frac{3}{4}$ —18·5	9 —15·6	9 $\frac{1}{2}$ —16·9
124	F.	57 $\frac{1}{2}$	15 $\frac{1}{2}$ —27	12 $\frac{1}{2}$ —21·7	12 $\frac{1}{2}$ —21·7	11 —19·1	8 $\frac{3}{4}$ —15·2	9 $\frac{1}{2}$ —16·5
125	F.	57	15 $\frac{1}{2}$ —27·2	13 $\frac{1}{2}$ —23·7	13 $\frac{1}{2}$ —23·7	10 $\frac{1}{2}$ —18·4	8 $\frac{1}{2}$ —14·5	9 $\frac{1}{2}$ —16·6

No.	Sex	Body	Femur	Tibia	Fibula	Humerus	Radius	Ulna
		L.	L.—P.	L.—P.	L.—P.	L.—P.	L.—P.	L.—P.
126	M.	57	15½—27·2	12¼—21·5	12½—21·9	10½—18·4	8 —14	9 —15·8
127	M.	57	16 —23·1	12 —21·1	12 —21·1	11 —19·3	8½—14·9	9½—16·6
128	F.	57	14 —24·6	12½—21·9	12½—21·6	10½—18·4	8½—14·9	9½—16·6
129	F.	57	15 —26·3	12 —21·1	12½—21·9	11 —19·3	8½—14·9	9 —15·8
130	F.	57	14 —24·6	12 —21·1	12 —21·1	10 —17·5	8 —14	9½—16·6
131	F.	57	16 —28·1	12½—21·9	13 —22·8	11 —19·3	9 —15·8	10 —17·5
132	F.	57	14 —24·6	12 —21·1	12 —21·1	10 —17·5	8 —14	9 —15·8
133	F.	57	14 —24·6	12 —21·1	12½—21·9	9½—16·6	8 —14	8½—14·9
134	F.	56½	14¾—26·1	12 —21·2	12 —21·2	11 —19·5	8½—15	9½—16·8
135	F.	56½	15 —26·5	12 —21·2	12½—22·1	11 —19·5	9½—16·8	10½—18·6
136	F.	56	15 —26·8	13 —23·2	13 —23·2	10½—18·7	8½—14·7	8½—15·6
137	F.	56	15 —26·8	12 —21·4	12½—22·3	10½—18·7	8 —14·3	9 —16·1
138	F.	56	15 —26·8	13 —23·2	13½—24·1	11 —19·6	8½—15·2	9½—17
139	F.	55½	14½—26·1	12 —21·6	12 —21·6	11 —19·8	8½—15·8	9½—17·1
140	F.	55	15 —27·3	13 —23·6	12½—23·2	11 —20	8½—15·9	9½—17·3
141	M.	55	15 —27·3	12½—22·7	12½—22·7	11¼—20·5	9 —16·4	9½—17·3
142	F.	55	14¼—25·9	13 —23·6	13¼—24·1	11¾—20·1	9½—17·3	9 —16·4

Table B

In this table the average lengths of the long bones in inches and their proportion to body length are given.

L. = length, P. = proportion to body length calculated to a scale of 100.

	Body	Femur		Tibia		Fibula		Humerus		Radius		Ulna	
		L.	P.	L.	P.	L.	P.	L.	P.	L.	P.	L.	P.
In Hindus													
Males	63·8	16·7	26·2	14·2	22·3	14·3	22·4	12	18·8	9·4	15·1	10·5	16·4
Females	59	15·5	—	13·2	—	13·3	—	11·1	—	8·8	—	9·7	—
Both sexes	62	16·2	—	13·8	—	13·9	—	11·6	—	9	—	10·2	—
In Europeans													
(Humphry)	65	17·88	27·5	14·4	22·15	—	—	12·7	19·54	9·2	14·15	—	—
(Tidy)	—	—	27·5	—	22·15	—	—	—	19·54	—	14·15	—	—

It will be observed from the previous tables that the average length of the long bones of the thigh and leg in males is greater than that of the females by about an inch, whereas in the case of the arm and forearm bones the difference is less, ranging from ·6" to ·9". The proportion to body length however is the same whether it is calculated from male or female bones. There has been a slight variation in the two sexes in the case of the tibia, fibula, humerus and radius, but this has been neglected as it did not exceed ·1 per cent. As there are no previous records of these measurements in India, I hope these observations will be of some use to Medical Jurists in India.

My grateful thanks are due to Professor Sir Arthur Keith for suggesting to me to take up this subject. I thank Dr Bipin Behari Bysak, Demonstrator of Anatomy, for his kind help in carrying out this observation.

## ANOTHER CASE OF HERMAPHRODITISM IN MAN

By A. GIRGIS, M.R.C.S. (ENG.), L.R.C.P., B.Sc. (LOND.).

A CASE was admitted to the Gynaecological Wards of Kasr-el-Eini Hospital, Cairo, under Doctor Mahfouz Bey, by whose courtesy I was able to make the following observations.

The object of reporting this case as an appendix to the two cases reported in the *Journal of Anatomy*, LVII, Part 3, April 1923, is the presence of a few more valuable points elucidated in this case, on account of the fact that microscopical and abdominal examinations were made.



Figs. 1 and 2. Full-face views of patient described in text.



The patient, aged 19, had been married for three years, and came to the Hospital for treatment for sterility. The patient said that coitus was not properly performed, and that "she" had no sexual feelings towards either sex. "She" has six sisters and two brothers, who are all apparently normal. "She" has a slight moustache, and "her" shoulders, breast, pelvis and features are those of a man (Figs. 1 and 2).

The vagina is short and narrow and ends blindly. No uterus or ovaries could be felt. Two tumours were present—one on either side of the symphysis



Fig. 3. Tumours in labia majora.

pubis, which could be pushed into the labia majora (Fig. 3). Labia minora are well-developed. The clitoris has been removed (circumcised) but shows a thick root. The urethra opens into a normal vestibule. There is no sign of hymen.

Note in Figs. 1 and 2, the pubis is prolonged downwards, giving the appearance of the corresponding part in man.

The following measurements were taken:

Antero-posterior diameter of outlet pelvis	9	cms.
Transverse of outlet	...	8½ "
External conjugate	...	16½ "
Intercristal	...	25 "
Anterior interspinus	...	20 "
Posterior interspinus	...	10 "
Intertrochanteric	...	28 "

The left tumour was removed and microscopically examined. It proved to be a testicle with a vas.

The testicle shows active spermatogenesis. The abdomen was also opened, and the absence of uterus, ovaries, tubes, prostate and seminal vesicles was confirmed. The testicle measured 4.2 cms. in length, and 2.2 cms. in breadth.

This case is of type "B," mentioned in my previous paper, i.e. the patient is an imperfect male. Again, whether this is a case of true, or pseudo-hermaphroditism cannot be said for certain, as the right tumour was not removed, though it felt and gave the sensation to the patient of a testicle, like the left one.

## TENSOR FASCIAE SURALIS

By D. BARRY AND J. S. BOTHROYD,

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of the University of Melbourne.*

THE *m. tensor fasciae suralis* is defined in Quain's *Anatomy* as being a muscular slip passing from one or other of the hamstring muscles to the fascia of the back of the leg. Its appearance in the human subject is sufficiently rare as to justify its description when met with.

In our specimen the abnormality occurred in a male subject, aged 70 years, and was present on the left side only. The muscle arose from two fascial slips, the one from the deep surface of the fascia lata of the middle of the flexor region of the thigh at the point of divergence of the biceps femoris and the semi-tendinosus, and the other from the fascia lining the deep and medial surfaces of the biceps femoris. These two slips of origin unite to form a tendon which, after a course of about one and a half inches, splits to enclose a flat muscular belly about three inches in length, which runs distally across the popliteal space immediately deep to the fascia lata. At the distal extremity of the muscular belly the two fascial slips of origin re-unite to form a tendon of less than an inch in length, which finally expands to become blended with the fascia over the gastrocnemius and the deep surface of the fascia cruris. The deep surface of the muscle is entered and supplied by a small artery from the femoral artery given off just proximal to the hiatus tendineus, and the nerve supply appears to be derived from the tibial nerve (internal popliteal).

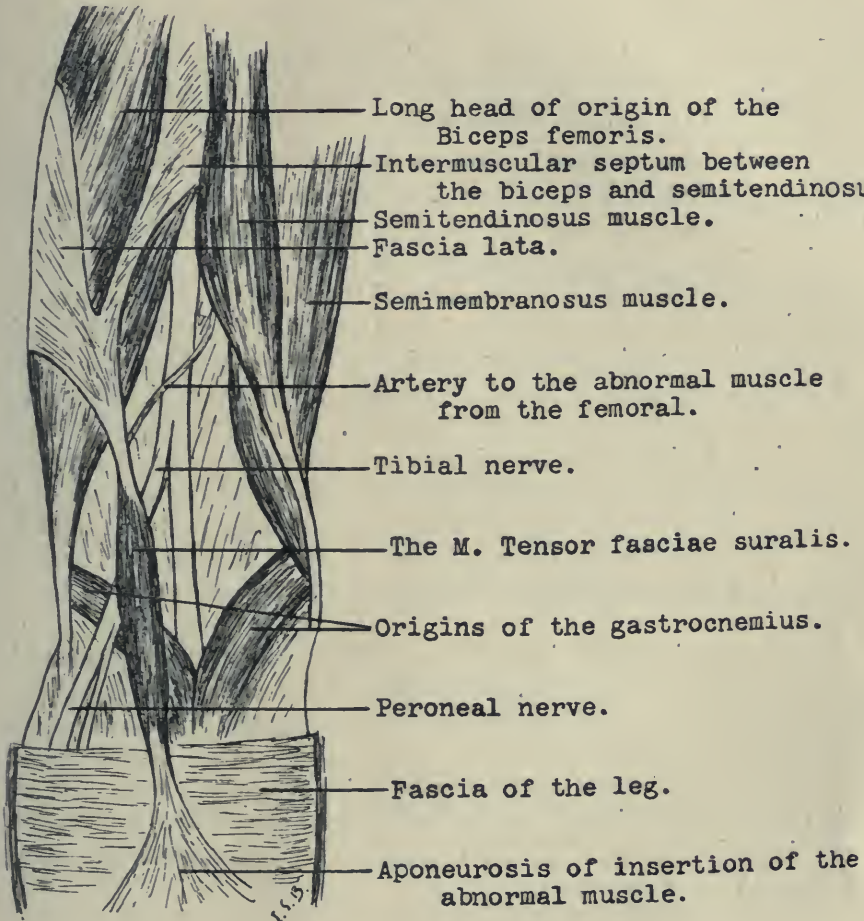
References to this rare abnormality are to be found in the *Journal of Anatomy and Physiology*, vol. VI, 1872, p. 442, where specimens recorded by Grüber (1871) and Turner are described. Vol. XV of the same journal, 1881, p. 296, contains W. D. Halliburton's case, in which mention is also made of the first recorded account of the variation by W. G. Kelch in 1813, as also of all three of Grüber's cases.

In the *Anatomical Record*, vol. VII, 1913, p. 3, J. Parsons Schaeffer describes an example of the muscle met with in the Yale Medical School during the session of 1911-12, and states that "Grüber, Halliburton, Kelch, Le Double, Testut, Turner, and others have observed supernumerary muscles of these regions." He adds that "the cases in which additional muscles appear in the thigh and sural regions are not very common."

The anomalous digastric muscle observed in the thigh of a Chinese, described by Paul H. Stevenson in the *Anatomical Record*, vol. XXIII, 1922, p. 281, does not appear to us to belong to the category of muscular variations here



dealt with, or if it does, it departs a good deal from the general type. He quotes Testut's summary of the eight or nine distinctive types reported in the literature up to 1911, from which it would appear that muscular anomalies in this region are very rare, probably not more than 15 or 20 having been



reported in the last century. The works of Testut and Le Double seem to suggest that when such abnormalities do occur, they are to be regarded as a reversion to the state of affairs found in many animals where the biceps femoris passes farther distally than it now does in man.

A more extended reference to the comparative anatomy of variations of the hamstring region is to be found in an article by Klaatsch in the *Anatomischer Anzeiger*, vol. xxxviii, 1911, p. 305, together with the description of a similar abnormality met with in the Anatomy Department at Breslau, while F. Pardi's *Muscoli tensores fasciae cruris*, published in Italy in 1909, apparently does the same, though this last has not been available to us in the original.

## REVIEW

*The Mammals of South Australia.* By Prof. FREDERIC WOOD JONES, D.Sc.  
Part 1. The Monotremes and the Carnivorous Marsupials. (Adelaide, 1923.) pp. 131, figs. 88. Price 4s.

This most valuable contribution to our knowledge of the Australian mammals, is issued as a "Handbook" by the South Australian Branch of the British Science Guild and published by favour of the Premier of South Australia—Sir Henry Barwell, K.C.M.G.—at the remarkably reasonable price of 4s. The author has given all students of Comparative Anatomy the best introduction yet written to the study of the mammalian fauna of the Australian continent; it is an original contribution in the true sense of the word. Prof. Wood Jones's colleagues at home are familiar with the exquisitely finished drawings with which he illustrates his papers. In this "handbook" he has adorned his text with drawings which for accuracy, clearness and freedom of line are examples of what illustrations should be. Whether he is rendering the external features and attitude of the curious living forms described in his text, or representing the details of skull structure or depicting the salient features of an elaborate dissection he seems to be equally at home in each instance.

We have mentioned the illustrations first, but they are only in keeping with an equally remarkable text. To do this justice would require an extensive review and involve pages of quotation. All the fundamental problems relating to the evolution of the various branches of the mammalian phylum are discussed anew in the light of fresh evidence which is here put forth. We must remain content with this brief notice, merely advising all who are interested in the enigmatical fauna of Australia to take steps to procure a copy of this work by Prof. Wood Jones.

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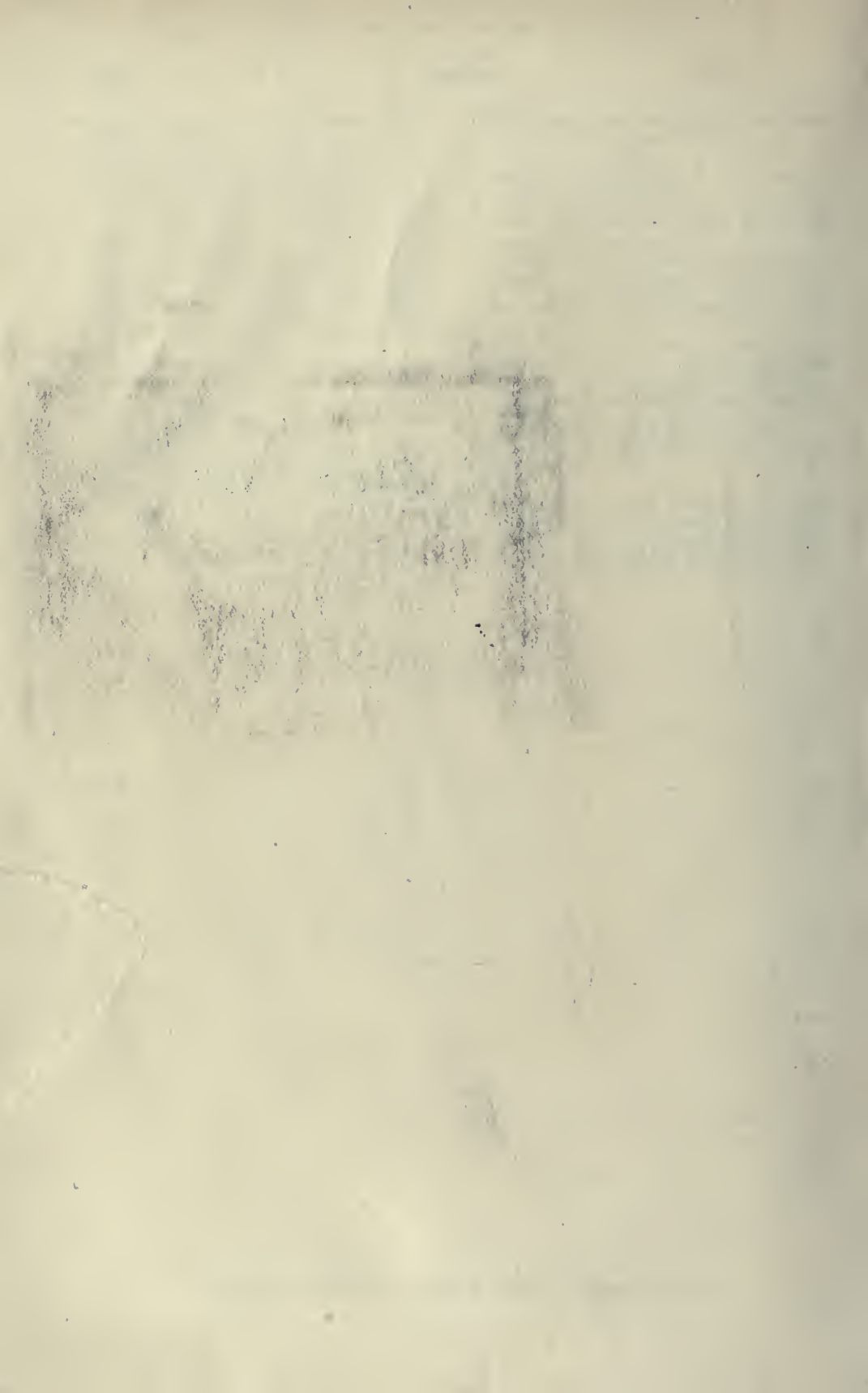




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